THE

BOTANICAL GAZETTE

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OF THE UNIVERSITY OF CHICAGO

ASSOCIATE EDITORS:

VOLUME XXXVI

JULY—DECEMBER, 1903

WITH TWENTY PLATES AND FORTY-EIGHT FIGURES AND MAPS

CHICAGO, ILLINOIS
PUBLISHED BY THE UNIVERSITY OF CHICAGO
1903

PRINTED AT
The University of Chicago Press
CHICAGO

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DATES OF PUBLICATION.

No. 1, July 16; No. 2, August 15; No. 3, September 15; No. 4, October 15; No. 5, November 15; No. 6, December 19.

ERRATA.

P. 62, last 2 lines for "which curved where it grew. Likewise in both root and shoot the curvature" read "which curved where it grew, likewise in both root and shoot. The curvature . . . ."

P. 132, line 6 from below, for de read der.

P. 150, line 21 from below, for nucleus read nucleolus.

P. 159, line 15 from below, for Bogoniensis read Bogoriensis.

P. 173, legend under fig. 4 after section insert through; and add, Vertical scale immensely magnified.

P. 177, legend fig. 5, add with its clapper.

P. 222, line 5 from below, for Pinos read Pinus.

P. 253, footnote 18, line 3, for archœology read archaeology.

P. 306, line 14, for 4.5μ read 4.5^{mm}.

P. 306, line 22, for 3.5μ read 3.5^{mm}.

P. 327, line 6, for is read are.

P. 377, line 10, for comprises read comprise.

P. 377, line 18, transfer first word, and, to beginning of line 19.

P. 378, line 6 from below, for atternifolia read alternifolia.

P. 396, line 20, for Jurrassic read Jurassic.

VOLUME XXXVI NUMBER 1

BOTANICAL GAZETTE

JULY, 1903

ON THE GAMETOPHYTES AND EMBRYO OF TAXODIUM.[1]

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY, No. 1.

W. C. COKER.

(WITH PLATES I–XI)

IN spite of the recent great increase in our knowledge of spermatogenesis in many groups of gymnosperms, this part of the life history of the Taxodieae remained, at the time this work was undertaken, almost unknown. A short contribution by Shaw ('97) on Sequoia had appeared in 1897, and Arnoldi ('99[a, b]) has recently added two papers on the development of the reproductive organs in Sequoia. These observers have cleared up many salient points in the development of this genus, but the group as a whole is still to be studied.

Taxodium itself, probably on account of its limited geographical distribution, has been greatly neglected by investigators. Coulter on the histology of the leaf, Masters on the seedling, Lotsy and Meehan on the knees, and Von Schrenk on the disease called "peckiness" are among the few papers that have been devoted, in whole or in part, to the study of Taxodium, and none is concerned with the development of the seed.

The present work was suggested by Dr. D. S. Johnson, to whom I wish to express my gratitude for his unfailing kindness and helpful advice throughout its prosecution. I also wish

[1] A dissertation submitted to the Board of University Studies of the Johns Hopkins University, June 1901, for the degree of Doctor of Philosophy.

publicly to thank my brothers for their assistance in sending me material at frequent intervals.

METHODS.

Collections of *Taxodium distichum* Richard, the only species studied, have been made for about three years, chiefly from Hartsville, S. C., but also from Baltimore, Md., and New Berne, N. C. Fixing has been done at the tree in all critical stages, but fresh material, sent in tight boxes from Hartsville to Baltimore, has frequently given good results. Flemming's strong solution, chrom-acetic acid solution, alcoholic solution of picric acid, saturated solution of corrosive sublimate in 95 per cent. alcohol have all been used to some extent; but a saturated aqueous solution of corrosive sublimate (95 or 90 parts) and glacial acetic acid (5 or 10 parts) has been generally used. The latter gives results that are scarcely, if at all, inferior to those obtained with the Flemming solution, while it is more satisfactory than any of the other fluids mentioned. In searching for protoplasmic connections between cells, Gardner's ('83) methods were used, but only with fixed material. Potassium iodid and chlor-zinc-iodid were useful in determining the presence of starch, and have been used throughout for this purpose. A number of stains have been tried, but Flemming's triple has been most used. Young cones were split, or the scales removed entire. In older cones the ovule was removed and the nucellus exposed by breaking off the lignified tip of the integument, or the whole prothallium was taken from the seed. Sections 5–10 μ thick were made by the usual paraffin method.

THE STAMINATE CONE.

The staminate flowers are born on short branches which are either simple or compound. If simple, these branches are usually longer and more numerous than if compound. They appear in the fall from near the tips of the branches of the same year, and at the beginning of October or even earlier the young staminate flowers may be seen in the axils of their scale-like leaves. A longitudinal section of a sporophyll at this time shows no distinction between primary archesporium and other

tissue, all the cells of the lower part of the sporophyll being of about the same size, and having dense contents. Soon, however, certain centrally placed hypodermal cells begin to divide by periclinal walls and give rise to rows of cells as shown in *fig. 1*. The outermost cells of these rows, by a periclinal division, form the one-layered tapetum and the inner layer of the sporangial wall. By division of adjoining cells the tapetal layer is extended completely around the sporogenous tissue (*fig. 2*), and by January, or earlier, the microspore mother-cells are formed and ready for their division in early spring. Chamberlain ('98) has reported a similar stage during winter in the microsporangia of Pinus, Cupressus, and Taxus. The cells of the whole sporophyll, with the exception of the tapetum and the sporogenous tissue, contain starch through the late fall and winter until renewed growth in spring alters its arrangement. In the middle of November the nuclei of the tapetal layer show a peculiar structure not found at other times. They have a very coarse and wide-meshed reticulum, upon which the chromatin is distributed in large granules of very unequal size. There is no nucleolus. The nuclei of the sporogenous tissue have several nucleoli and a thinner reticulum than at a later stage.

No trace of an indusium-like outgrowth from the sporophyll is present for the protection of the sporangia, such as occurs in Cupressus, Thuja, and species of Juniperus. During early stages of development the cells of the upper part of the sporophyll are completely filled with a peculiar homogeneous substance staining bluish with gentian, which, as its subsequent history shows, is either a form of starch or an intermediate product in the formation of starch. It is not stained blue by iodin. At the stage of *fig. 1*, this substance is being replaced by starch grains of the usual kind, and a direct relation in amount between the two is evident, the starch appearing in proportion as the amorphous substance disappears. The cells on the line of transformation contain both starch and amorphous substances in proportionately smaller quantities.

Before their division in the spring, the pollen mother-cells become filled with starch, while the grains in other parts of the

sporophyll are being rapidly corroded. The persistence of this starch in the mother-cells during division and its disappearance as the exine is formed in the pollen grain agrees with what is already known in cycads and conifers. The ripe pollen grain contains no starch, nor is any found in the pollen tube until it appears in the protoplasm of the central cell shortly before the formation of the sperm cells. The number of microsporangia on a sporophyll may be as many as nine, seven being a common number. The wall of the mature microsporangium consists of but two layers of cells on the exposed surface, and in this respect Taxodium differs from the Abieteae, Taxeae, Cycadales, and Ginkgo, and agrees with the Cupresseae and Gnetales. The cells of the outer layer of the wall have the sides and inner faces strengthened by bands of cellulose, while those of the inner layer are very much flattened and poor in contents. The cells in the tapetum have very dense contents and are shorter and thicker than those of the inner wall. They disorganize at about the time that the division occurs in the pollen grains.

The division of the pollen mother-cells took place this year (1901) in South Carolina on March 6th, and both divisions were found on the same day, even in the same cone, but the stages found in the same sporangium are not quite so different as Coulter and Chamberlain ('01) figure for *Pinus Laricio.* Changes of the nucleus leading up to the first division were not present in my material, but good preparations of all stages during and subsequent to the metaphase of the first division show that the phenomena are similar in all essential respects to those described in detail by Strasburger ('00) for Larix.

The chromosomes, as arranged on the nuclear plate, are short and thick (*fig. 3*). They stand at right angles to the axis of the spindle, the fibers being attached to the inner ends. The splitting begins at the point of attachment and in favorable cases the line may be seen between the two halves in the as yet unseparated outer limb. Very soon after the splitting is completed and the daughter chromosomes begin to move to the poles, the fibers are seen to be attached to the middle of the

bent chromosomes and the inner ends of the latter are composed of four arms, lying side by side, and generally of the same length (*figs. 4–6*). The second splitting has evidently occurred and the arrangement is now just as in Larix as described by Strasburger ('00). The chromosomes remain thick and short as they approach the poles, and their number can be easily determined to be either eleven or twelve. Eleven are shown in *fig. 6* in polar view, and at least this number could be distinctly made out in other cases. Sometimes there seem to be twelve, but on account of the crowding in such cases I have never been sure of this number. Twelve chromosomes have been found by Belajeff ('94) and Strasburger ('92) in the pollen mother-cells of *Larix europaea*, by Blackmann ('98) in pollen mother-cells and oosphere of *Pinus sylvestris*, by Juel ('00) in the megaspore mother-cell of *Larix sibirica*, and by Chamberlain ('99) in the pollen mother-cells, endosperm, and jacket cells of *Pinis laricio*. It would thus seem from analogy that the number of chromosomes in the pollen mother-cells of Taxodium is also twelve rather than eleven.

The daughter nuclei (*fig. 7*) before the next division enter into a fairly well-developed resting stage. There is a distinct reticulum, if indeed a rather coarse one, and the chromatin is grouped in larger masses than in the reticulum of many resting cells, approaching more nearly the condition already described in the nuclei of the tapetal layer of the microsporangium in November. Strasburger ('00) describes such a condition in Larix, but tries to bring it in harmony with other cases by considering the network as spun out from the chromosomes. His distinction is not clear to me, and I think it must be acknowledged that the daughter nuclei of the first division may, at least in some cases, reach before their next division a relatively well advanced resting stage. From *fig. 7* it will be seen that the cell walls of the mother-cell have not disappeared at the time of tetrad-formation. In places the walls have begun to go to pieces, but in others remain entire and in close contact with their neighbors. No case was found where the final divisions were bilateral, as is sometimes the case in *Pinus Laricio* (Coulter and Chamberlain, '01).

The connecting fibers of the first spindle produce a distinct cell-plate, extending entirely across the cell before the nuclei have begun to divide a second time. On each side of the plate the starch grains are densely crowded. The chromosomes of the second division are single slightly curved rods, and are evidently of about the same size as the halves of the double chromosomes of the first division. The starch begins to disappear during the second division of the pollen mother-cell, and is completely used up during the formation of the exine of the pollen grains, which becomes quite evident in about three days after the last division. The nucleus of the fully formed but yet undivided pollen grain is evenly and coarsely granular and generally without a nucleolus (*fig. 8*).

About ten days after its formation the pollen grain divides. The spindle is very small and the chromosomes are proportionately longer than in the reducing division (*figs. 9* and *10*). This is the only division of the pollen grain, no sterile prothallial cell being formed, and it separates at once the generative cell from the tube cell. The former is flattened lens-shaped, concave toward the inside, and furnished with a distinct *Hautschicht* (*fig. 11*). This division occurs a few days before the pollen is shed, and it is in this condition that the ripe pollen reaches the nucellus (*fig. 12*). In the absence of any sterile prothallial cells, Taxodium agrees with the Cupresseae and Taxus, and differs from all other conifers and cycads. The number of sterile prothallial cells in the pollen grain of gymnosperms has been determined in the following cases: two in Ginkgo (Strasburger, '92), *Larix europaea* (Strasburger, '84), *Picea vulgaris* (Belajeff, '93), *Pinus silvestris* (Strasburger, '92), *Pinus Pumilio* (Coulter and Chamberlain, '01); one in Ceratozamia (Juranyi, '82; he occasionally found two in *C. longifolia*), Zamia (Webber, '97), Cycas (Ikeno, '99); none in Biota, Cupressus, Juniperus (Strasburger, '92), *Taxus baccata* and Juniperus (Belajeff, '93).

The great importance of correctly determining the number of divisions in the pollen grain has not been overlooked, and repeated sections, at all stages of the development of the pollen

from the mother-cell stage to the sprouting of the pollen tube, have been made from collections obtained in both 1900 and 1901, and I think it certain that there is but one division of the pollen cell in Taxodium.

THE POLLEN TUBE.

The first indication of sprouting is given by the swelling up of the generative cell into the tube cell, and by an increase in size of both nuclei (*fig. 13*). The exine is usually thrown off at an early stage, as shown in *fig. 14*. In this figure the nuclei of the pollen tube have not changed their position, the tube nucleus lying immediately above the generative cell. The pollen tube contains no starch, either now or during its course to the prothallium. As the tube advances, the tube nucleus moves from its position over the generative cell and passes slowly down toward the tip. Indications of branching are soon seen in the pollen tube (*figs. 17, 29, 22, 23*). In *fig. 16* the generative cell seems by its position to be bounded by an actual membrane, but no indication of a cellulose wall was obtained, and if one is present it is exceedingly thin and quickly dissolved. By comparing *figs. 15* and *16* it will be seen that the sprouting does not take place at any definite point in reference to the position of the generative cell.

The division of the generative cell does not occur until several weeks after the sprouting of the grain (*figs. 19–21*). The stalk nucleus soon loses its definite hold upon the protoplasm around it, although immediately after the division (*fig. 19*) it is still bounded by a distinct protoplasmic sheath. The central cell retains the characteristics which mark the generative cell before division. It is furnished with a distinct *Hautschicht* and has the shape of a double convex lens. It will be noticed that immediately after the division the stalk cell is larger than the central cell. Belajeff ('91, '93) describes these two cells as being of equal size in Taxus. In *Juniperus communis* he ('93) finds the outer cell to be smaller, while in *Picea vulgaris* the opposite is true. There is not much difference in size in *Pinus Laricio*, as figured by Coulter and Chamberlain ('91). It will thus be seen that Taxodium agrees with Juniperus in the relative size of the stalk and central cells immediately after their formation.

Belajeff ('91, '93) describes the stalk nucleus as passing the central cell as it wanders down the tube. Such a description could hardly be applied in Taxodium when the tube is at right angles to the axis of the spindle of the generative cell. The stalk nucleus is as near the tip of the tube as is the central cell, and they both wander down together until they reach the tube nucleus (*fig. 22*). It will be seen from *fig. 26* that the three nuclei of the pollen tube can easily be distinguished at this stage. The stalk nucleus is smaller than the tube nucleus, while the protoplasm of the central cell is distinct from that of the pollen tube. The stalk and tube nuclei now advance slightly ahead of the central cell (*fig. 23*), and this relative position is retained by the three nuclei throughout the subsequent history of the pollen tube. In *fig. 23* the stalk nucleus is still slightly smaller than the tube nucleus, but the structure of the two is the same. The male nucleus is very like the other two, its nucleolus being slightly smaller.

The pollen tube proceeds to the prothallium without interruption; the growth, however, is much slower in the upper part of the nucellus than in the lower. No particular tissue of the nucellus tip is set apart to nourish or guide the pollen tube. All of its cells contain more or less starch, but there is no grouping of starch in definite areas. The pollen tube may reach the megaspore before the formation of a cellular prothallium (*fig. 25*). So early an approach of the pollen tube to the sprouting megaspore has not been described in any other case, so far as I am aware. Jäger ('99) gives one figure of *Taxus baccata* showing a pollen tube almost in contact with a young prothallium, and I have found that in *Taxus baccata canadensis* the pollen tube may reach the level of the megaspore before the latter has divided even once. One case was found in this plant where the pollen tube has grown against and badly compressed the megaspore before the latter had advanced far beyond the sixteen-cell stage. It was so completely crushed that the stage could not be exactly determined.

Fig. 26 gives the structure of the contents of the pollen-tube at a slightly later stage than *fig. 25*. The two free nuclei are

now exactly similar and lie side by side immediately beneath the central cell. The latter has increased greatly in size, as has also its nucleus, and the protoplasm is seen to possess a radiate structure. We find in the nucleus of the central cell a distinct peripheral network, and a nucleolus, irregular in outline and evidently of a compound nature. This kind of nucleolus, which we here meet for the first time, will be found to occur also in the nucleus of the central cell of the archegonium. In one case the central cell was at the tip of the pollen tube, with the two free nuclei behind it. One of the latter was pressed so closely to the protoplasm of the central cell as to indent it slightly. Such an abnormal relation between the generative and free nuclei has been noted in *Pinus Laricio* by Coulter ('97).

The further changes in the central cell before its final division into the sperm cells are so remarkable and have been so neglected in other conifers studied that I shall go into them with some detail. *Fig. 27* represents the central cell after it has reached its full size. It is no longer spherical, but has become elliptical in section, the long axis being perpendicular to the axis of the tube. The protoplasm is seen to be radiating from the two poles of the long axis. At these poles are sometimes to be distinguished slightly more granular areas, from which the radiations seem to diverge. The protoplasm is very dense, finely granular and in thin sections can be seen to have a reticulate structure. The faint areas at the poles of the cells will at once suggest in position the blepharoplasts of Ginkgo, Zamia, and Cycas. In reality, the resemblance is entirely confined to their position. Dr. Webber has kindly shown me his preparations of blepharoplasts in Zamia, and their intense staining and large size make further comparison impossible.

The nucleus, which is about half of the diameter of the cell, has rather abundant reticulum and a fragmented nucleolus. In addition to these, there has appeared a finely granular material which does not seem to differ in any respect from the linin material in the egg nucleus to be described below. It is most abundant around the nucleolus, but extends to all parts of the nucleus. In *fig. 27* one of the free nuclei is seen closely appressed

to the *Hautschicht* of the central cell; the other free nucleus does not appear in the section. This is about the latest stage at which these free nuclei retain their normal structure. They very soon begin to go to pieces, and the protoplasm of the pollen tube at the same time begins to disorganize. It becomes more homogeneous and retains more tenaciously the safranin stain. The nucleoli and chromatin of the free nuclei become more or less broken up and collected into masses of different size, a process which we shall see corresponds exactly to what occurs in the nuclei of the jacket cells of the archegonium shortly before its final division. Concomitantly with the disorganization of the nuclei and cytoplasm of the pollen tube, there becomes evident in the cytoplasm of the central cell a number of bodies staining a deep red in safranin. They resemble exactly the plastin granules that we have seen to appear at the disorganization of the free nuclei, and that they are actually transferred from the latter into the central cell seems possible. *Fig. 28* is a central cell after the appearance of these granules. They are arranged in a circular manner at some distance from the nucleus, and it may be that this distribution is connected in some way with the concentric arrangement of the fibers. At the time of the appearance of the plastin granules in the protoplasm of the central cell, there seems to be a distinct connection at the base of the cell between its protoplasm and that of the disorganizing material beneath it. Hirase ('95) describes large bodies lying in the protoplasm of the central cell of Ginkgo between the nucleus and the blepharoplasts. Webber ('97) confirms this and says that in addition to the two large bodies smaller masses of similar material were observed in other localities of the cell. He speaks of them as extra-nuclear nuclein. It is easy to compare these bodies with those of Taxodium. They stain deeply with safranin in both cases, the principal difference being that in Ginkgo they are generally fused into two large masses which occupy a definite position in the cell.

The disorganized mass of nuclei and protoplasm at the tip of the tube never completely disappears before fertilization, and it may appear in the tip of the archegonium above the protoplasm

of the egg after fertilization. In *fig. 28* a number of scattered starch grains have made their appearance in the cytoplasm of the central cell. They retain their scattered position until finally arranged into the dense starch sheath immediately surrounding the nucleus of the sperm-cell.

Changes in the nucleus preparatory to the final division of the central cell had already begun at the stage represented in *fig. 27*. In *fig. 28* these changes have proceeded still further. The chromosomes are being prepared from the few thick conspicuous threads that are present. The linin granules have become organized into a reticulum, and this reticulum seems to be arranging itself as if in the preparatory stages of spindle formation.

No attempt was made to study in detail all stages of spindle formation in the division of the central cell, but in *fig. 29*, which shows an oblique view of the spindle, the formation of its fibers from the nuclear reticulum and the granular nature of the more peripheral fibers seems evident. This formation of the spindle from the fibers of the nucleus will be described in more detail in the division of the ventral canal cell. *Fig. 30* shows a late telophase in the division of the central cell, the connecting fibers still being evident. A clear area is noticed on each side of the cell plate, and this area later extends entirely around the sperm cells. The starch and plastin material are collected at the distal ends of the spindle, but after the separation of the two daughter cells the starch becomes arranged in a dense sheath immediately surrounding the nucleus (*fig. 31*). Just outside of this sheath the plastin granules form a more or less complete layer. Beyond them is found the clear area previously mentioned, and the surface is composed of a distinct membrane which sharply defines the sperm cells from the protoplasm of the tube. After the formation of the daughter nuclei, they again begin to fill with the linin granules or reticulum (the so-called metaplasmic substance of Strasburger) until, at the time of maturity, they are so dense as to make any distinction between the granular material and chromatin reticulum very difficult. A small nucleolus, however, can be dimly discerned (*fig. 31*).

The sperm cells are now mature, and fertilization almost immediately takes place. I think it probable that the sperm cells do not round themselves off completely until after the bursting of the pollen tube, for although sometimes separated as much as a quarter of their diameter from each other, I have never seen them while still in the tube without a flat face on the inner side. This remarkably complex structure of the sperm cell distinguishes Taxodium from any phanerogam hitherto described, with the exception of Ginkgo and the cycads.

Recent work on the conifers, which in the structure of the male gametophyte approach Taxodium, gives very little detail as to the structure of the sperm cells. In Taxus Jäger ('99) mentions radial striae in the periphery of both the sperm cell and its smaller, functionless sister cell, but gives no further details of the protoplasmic structure. Arnoldi ('98) says that in Cephalotaxus the protoplasm of the sperm cells, which are here of equal size, is densest around the nucleus. In his work on Sequoia ('99) he gives no details of the protoplasmic structure of the sperm cells, but says they resemble those of the Cupresseae. Blackman ('98) makes some interesting observations on the sperm cells of *Pinus silvestris*. He says: "It cannot be doubted that cytoplasm also passes over into the oosphere, for each generative nucleus in the pollen tube is clearly surrounded by its own layer of cytoplasm, as can be observed in the stage when the tube is already in contact with the oosphere." Also, "it may here be noticed that small bodies staining deeply with fuchsin S may be observed in the generative cell protoplasm." These, he says, resemble leucoplasts. "If leucoplasts are really present in the cytoplasm belonging to the generative cells, the general view that the male cell brings over no plastids to the egg appears to be directly contradicted." This is the only mention I have seen made of a distinctive protoplasm belonging to the male cells in any of the Abieteae.

Neither Belajeff ('91, '93) nor Strasburger ('79, '84) describe the structure of the sperm cells of the Cupresseae in detail, but in gross structure they seem almost identical with those of Taxodium. Strasburger ('84) says that the pollen tube of Juni-

perus contains very little starch at time of fertilization, and thinks it therefore the more remarkable that the fusion nucleus should be surrounded by so much starch. From comparison with Taxodium, however, it seems probable that starch is also present in the sperm cells of the Cupresseae and has heretofore been overlooked. We shall see that a comparison of the processes of fertilization in the two cases strengthens this view.

The tip of the pollen tube has not been found to possess a distinct pit, such as is described by Goroschankin ('83), Dixon ('94), and Blackman ('98) in other conifers. The whole tip of the tube is furnished with a thinner cell wall than is found above, and if any pit occurs it is rendered less conspicuous by the thinness of the adjoining wall.

THE OVULATE CONE.

In October of the year preceding the ripening of the seed, the ovulate cones of Taxodium appear as very inconspicuous axillary buds on shoots of the same year. They usually occupy positions near the tip of the branch, and vary greatly in the number formed. It has usually been said that the ovulate cones are borne two or three together at the tip of branches which have also produced, further down, branches of the staminate inflorescence. While this is sometimes the case, and frequently so in trees examined in Baltimore, in its more natural habitat the ovulate cones are situated on branches of their own, and occur in much greater numbers than described. As many as fifteen or twenty mature cones have been found closely crowded on a fertile branch, and while this is the exception, as many as eight or ten are frequently grouped on vigorous trees. The ovulate cones replace the dehiscent short branches. The latter do not appear in the axils of all the scale leaves during the first year, but in only about one-third of them. The next year they are found in axils of leaves which were not occupied the previous year, but in following years they come from supernumerary axillary buds, and in the more slowly growing parts of the tree may appear year after year in the axil of the same scale leaf.

Fig. 32 shows a megasporophyll collected October 3, 1899.

In the axil of the sporophyll two swellings are present, the section passing longitudinally through one of them. These are the rudiments of the ovules which by January 4 (*fig. 33*) have begun to show the first indication of an integument. *Fig. 34* shows a sporophyll collected in Baltimore March 11. The ovule has increased in size and the nucellus and integument are of equal height. It seems that slow growth is continued all through the winter months whenever the condition of the weather will permit. A few weeks before the time of pollination, the placental outgrowth begins to appear as slight projections between and at the sides of the sporangia. By April 8 (*fig. 36*) the cushion has begun to show between ovule and scale, and by April 22 (*fig. 37*) it has reached a considerable size. The further development of the sporophyll is almost entirely confined to its basal part where cushion and scale are indistinguishable, and to the great extension of the cushion above and sidewise as a protective covering to the ovules. The tip above the cushion remains small and is soon much surpassed by the latter, which by fusing with the scale above soon comes to inclose completely the cavity in which the ovules lie. The outgrowths are not confined to the ovule-bearing scales, but are developed in almost as great degree in the axils of the adjoining scales below and at the tip. The number of fertile scales is usually about ten. They are bounded beneath and above by scales differing from them only in the absence of ovules. As the growth proceeds, the area of attachment of the ovules to the scale becomes much greater in extent, so that when the seed is mature almost the whole of its outer face is attached to the inner face of the scale.

This is not the place for a discussion of the homologies of the so-called placental cushion, and I shall confine myself to the expression of my belief that it is a new formation for the purpose of closing the opening between the scales for the protection of the ovules, and is not derived either from fused leaves or from a second integument of the ovule.

At the time of pollination the tip of the integument is composed of about three layers of cells, but immediately after pol-

lination the inner cells near the tip begin to grow in at certain points, and approaching the center almost completely close the micropylar cavity (*fig. 37*). There soon begins to appear in the tip of the integument an irregular ring of lignified cells with thick and pitted walls, which serves to strengthen this exposed end (*fig. 49*).

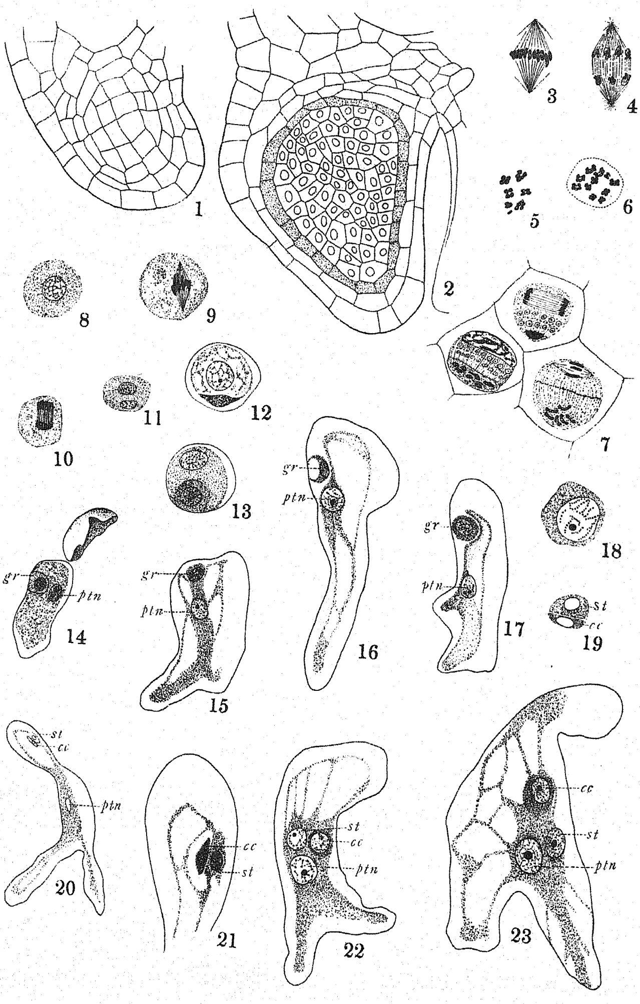
THE MEGASPORE.

The megaspore mother-cell cannot be distinguished from its neighbors until shortly before pollination. It is the basal or next to the basal cell of one of the distinct cell-rows which are evident in the center of the nucellus, and is situated at the same level as the point of insertion of the integument (*figs. 35, 37*). In this respect Taxodium agrees with the Cupresseae and differs markedly from Sequoia (Shaw, '96). At the time of pollination the megaspore mother-cell is slightly larger than the cells immediately surrounding it. Only a single megaspore mother-cell is present at this stage, but one case was found (*fig. 50*) in which the nucellus contained two young prothallia, one of which was larger than the other. Whether these were derived from two mother-cells or from the same mother-cell is a matter of conjecture. In this respect also Taxodium is seen to differ from Sequoia, in which Shaw ('96) and Arnoldi ('99[b]) have found it the rule for a number of prothallia to be developed. Hofmeister ('51) mentions the occasional presence of two prothallia in *Pinus silvestris* and *Taxus baccata* (confirmed since by Farmer ['92] for Pinus and by Jäger for Taxus), and I have found two in Podocarpus and *Taxus baccata canadensis*. With these exceptions the development of more than one prothallium has not been observed in the conifers.

The mother-cell increases slowly in size after pollination, and in about ten days the first division occurs. *Fig. 39* is a mother-cell shortly before its first division. It is abundantly supplied with starch grains, as are also the adjoining cells for about one layer. It will be seen that the nucleus is in synapsis, the meshwork being in a contracted mass near the nucleolus. Such a synapsis is found by Juel ('00) at the same stage in *Larix sibirica*. He also mentions the presence of denser fibrous areas at

either end of the cell near the nucleus. These areas are frequently to be noticed in the megaspore of Taxodium, but I have not been able to establish any definite relation between them and the spindle-formation (*figs. 38–43*). A slightly younger stage is shown in *fig. 38*, where the nucleus is of the usual structure and has not approached the tip of the cell, in which position it is always to be found before the first division. Stages of the first division are shown in *figs. 40–42*. The chromosomes were not counted, but are evidently not far from twelve in number. This division cuts off a large lower cell and a much smaller upper cell. The lower cell immediately prepares to divide again. The second spindle is shown in *fig. 43*, and in *fig. 44* the division is complete. The starch has begun to disappear during these divisions, but some is present until the conclusion of the second. Strasburger ('79) describes it as disappearing in *Larix europaea* before the second division; the same is true in *L. sibirica* (Juel, '01) and *Pinus Pumilio* (Coulter and Chamberlain, '01).

The upper of the two cells formed at the first division does not divide again, and its nucleus never reaches the resting stage, or indeed approaches it. *Fig. 42* shows the difference in the nuclei of the upper and lower cells of the first division. The lower is developing as usual, but the upper has formed no reticulum, and in fact never reaches a more highly organized stage. Its chromosomes remain fused and lumped, and soon present merely a disorganized, homogeneous appearance. This history of the upper nucleus is repeated in detail by that of the upper cell of the second division. There are thus formed in Taxodium only three cells from the division of the megaspore mother-cell, but as the lower divides twice, it is in every respect the equivalent of a pollen grain, as much so as if the upper cell of the first division had divided, as is the case according to Juel ('00) in *Abies sibirica*. Strasburger ('79) gives three, or seldom more, as the number of potential megaspores derived from the mother-cell in Taxus. He also gives the same number in *Larix europaea*, but as Juel has found four in *L. sibirica* it is possible that Strasburger may have overlooked one in *L. europaea*. Coulter and



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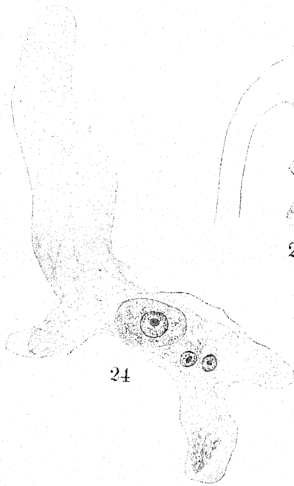
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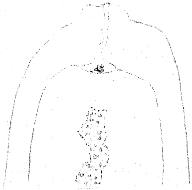
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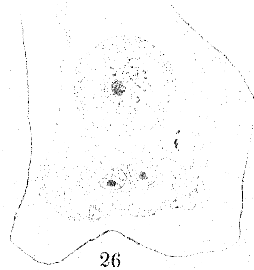
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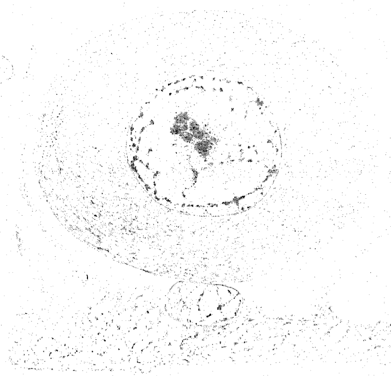
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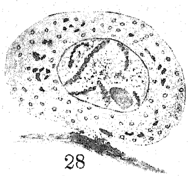
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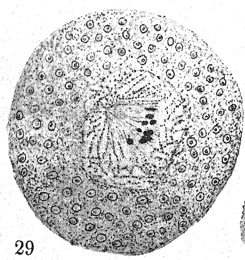
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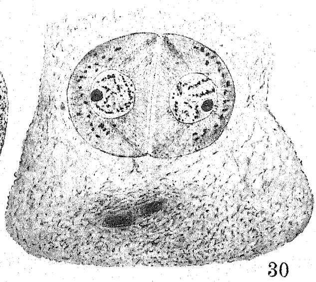
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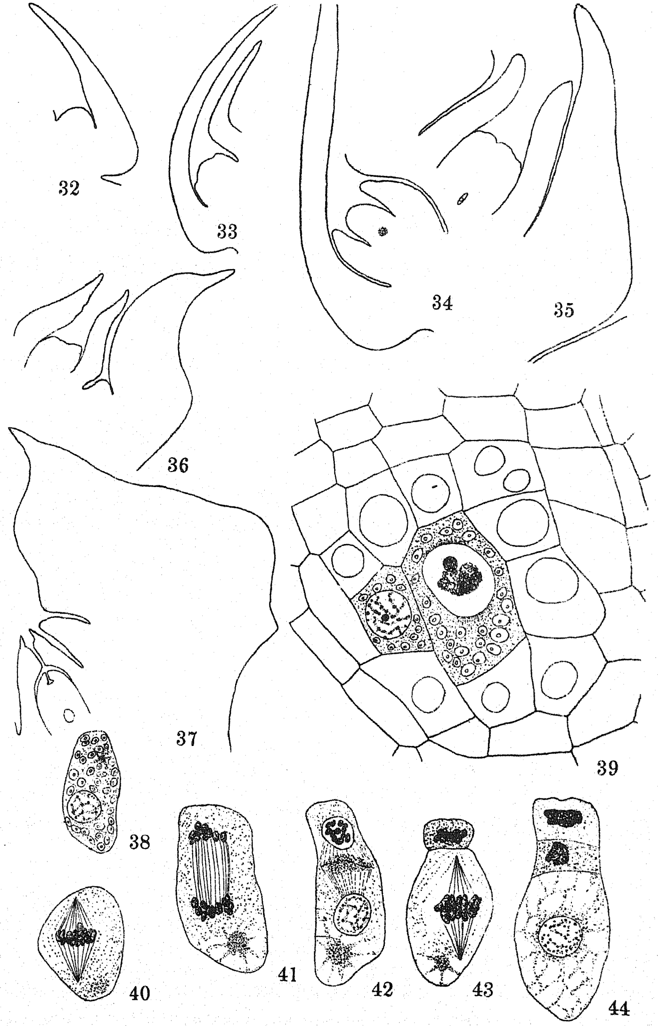

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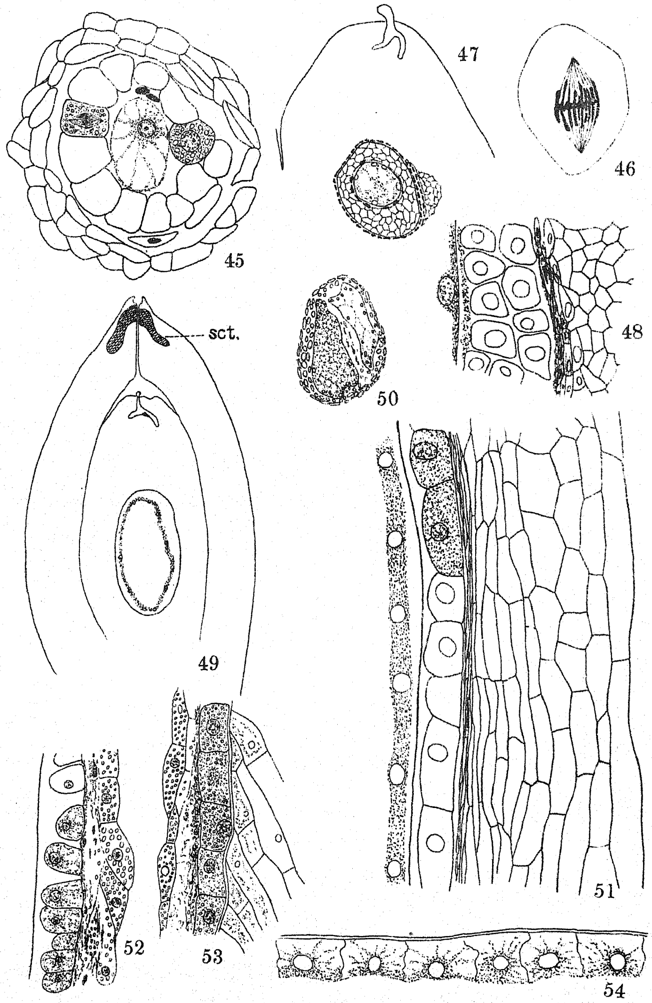

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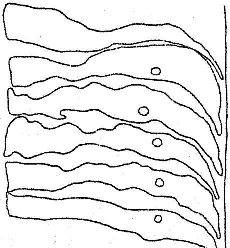
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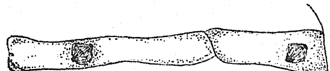
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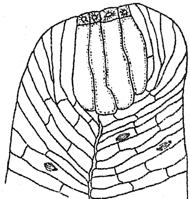
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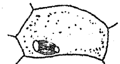
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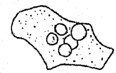
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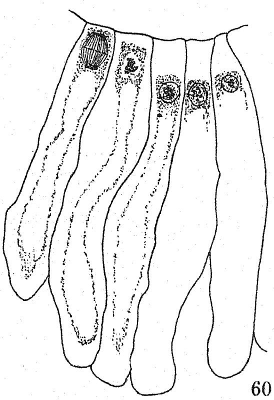
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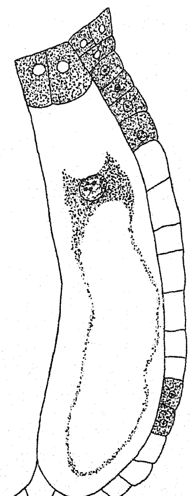
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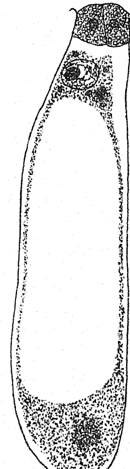
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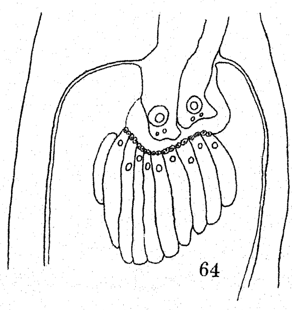
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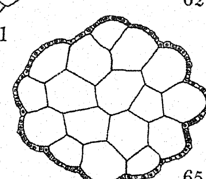
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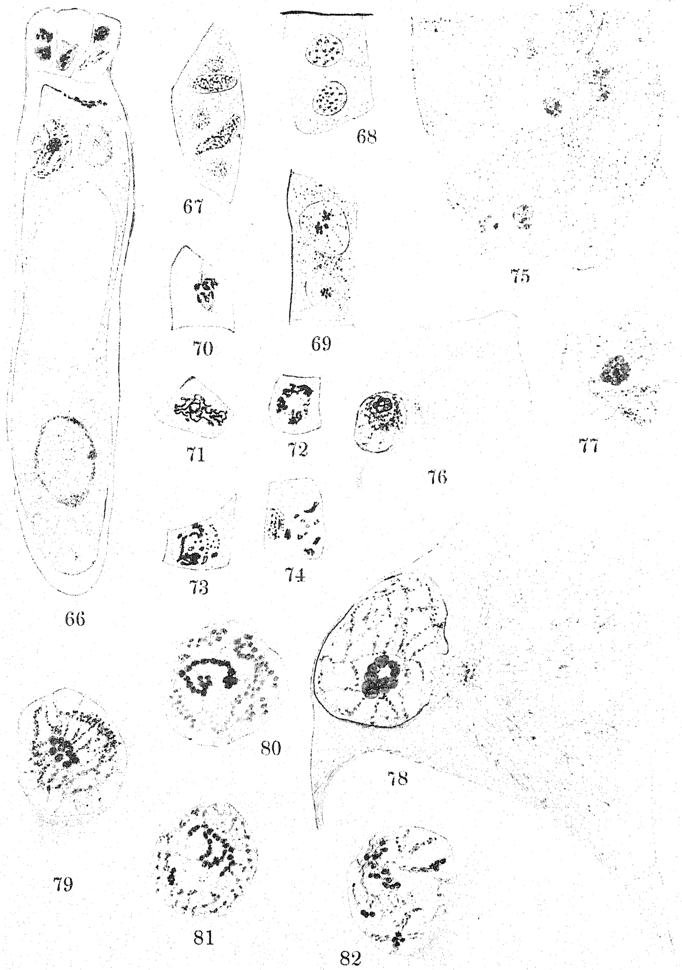

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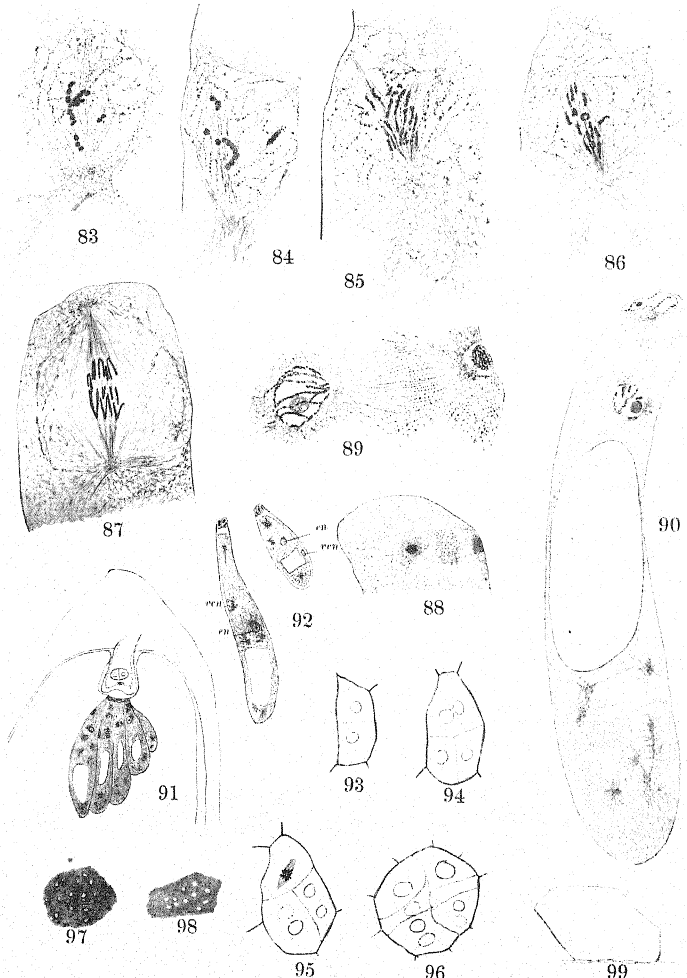

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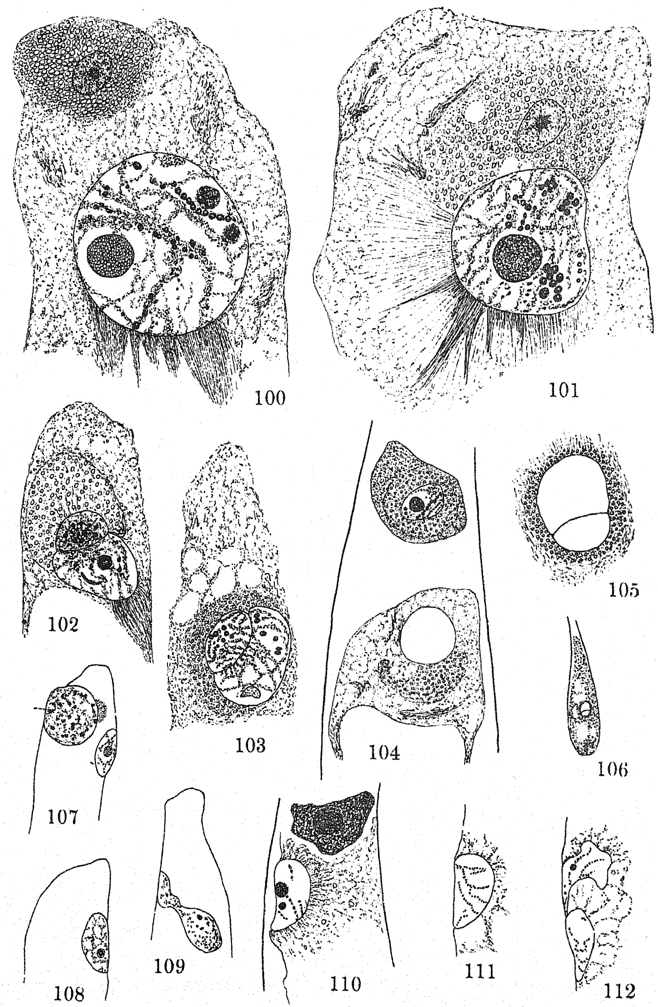
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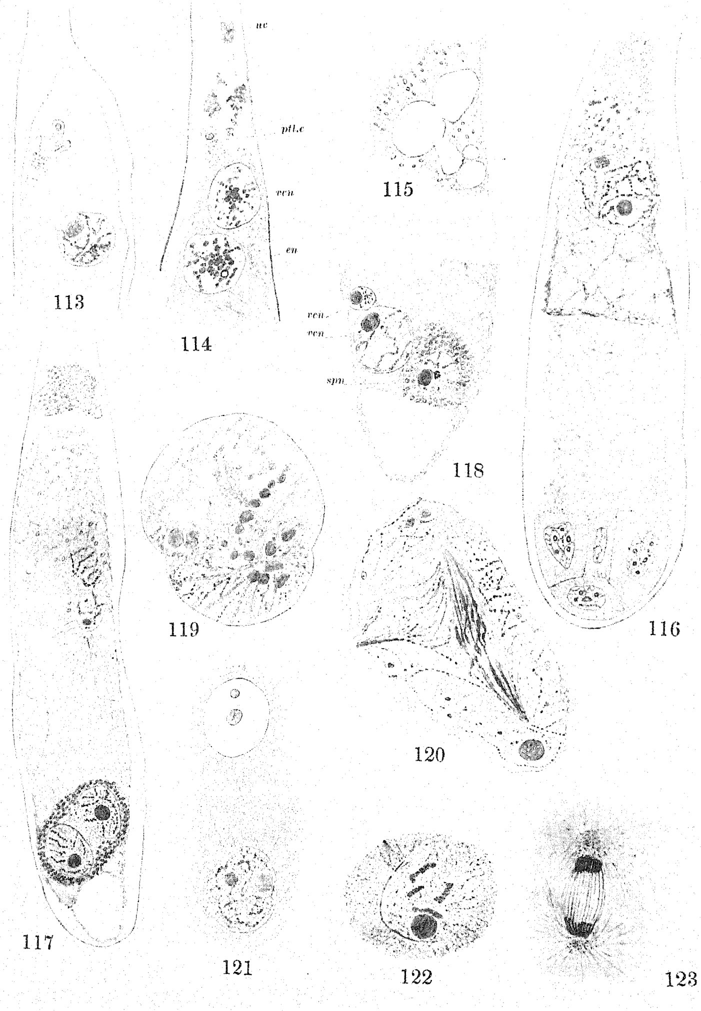

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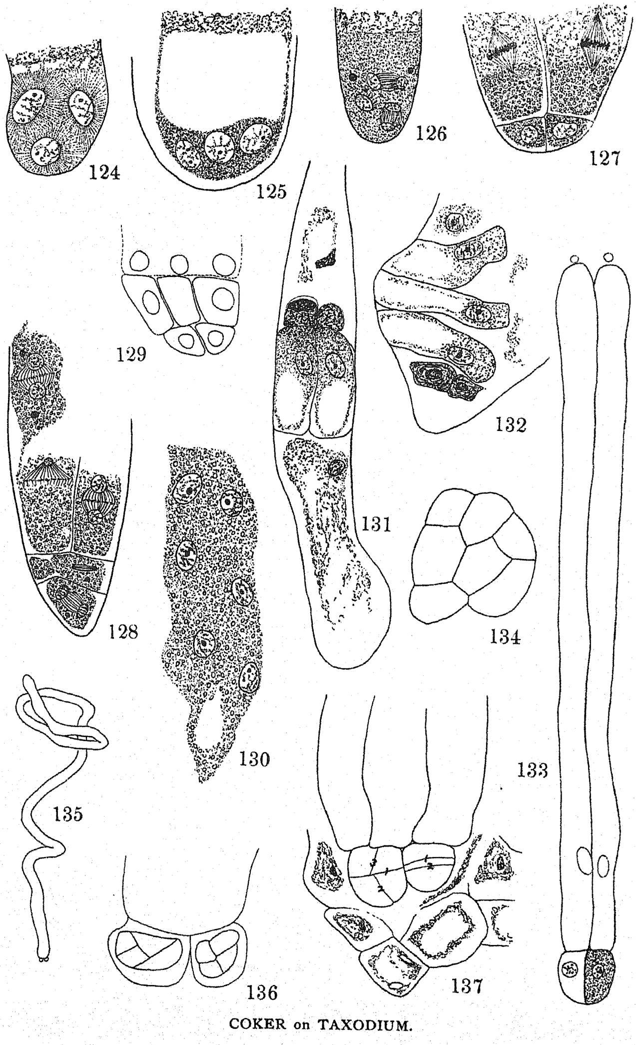

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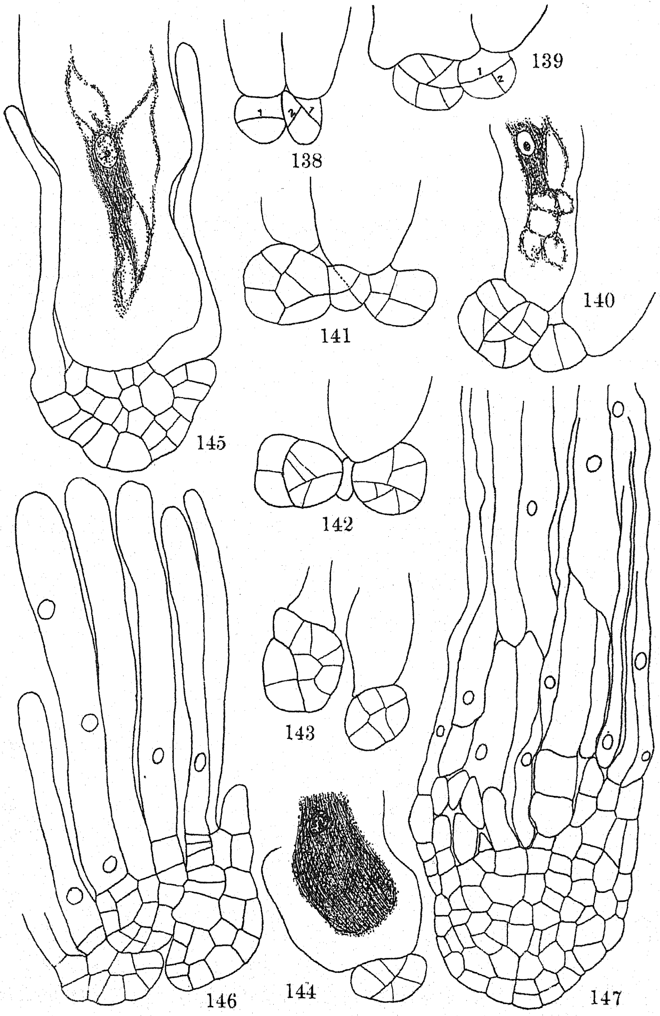

COKER on TAXODIUM.

Chamberlain ('01) also report four potential megaspores in *Pinus Laricio*, and Shaw ('96) has given the number as four in Sequoia. Almost nothing is known of the divisions of the megaspore mother-cell in the Cupresseae beyond Strasburger's remark that in Thuja the origin of the prothallium is essentially as in Taxus.

THE LARGE-CELLED TISSUE OR TAPETUM.

The cells immediately adjoining the megaspore mother-cell, as before stated, contain starch (*fig. 39*). After the megaspore is formed and begins to increase in size, the number of these dense, starch-containing, much enlarged cells is found to be greater (*fig. 45*). In *fig. 39* the transition between the starch-containing cells and the ordinary tissue around them is not very abrupt, but in *fig. 45* the boundary between the two has become distinctly marked. The larger cells are in close contact, their cell walls are intact, and their nuclei are large and apparently perfectly normal. Indeed, one of them is dividing mitotically, and they are not infrequently found dividing at this stage. *Fig. 46* shows such a cell in division. The spindle is placed centrally in the cell—not at one end, as in the division of the spore mother-cell—and in one case a cell-plate is being formed. The chromosomes were not counted, but the number is much more than twelve. The division seems to be an ordinary typical one. The cells immediately beyond the large-celled tissues are distinctly flattened and seem to be crushed by the cells within. On the lower side the nuclei of the nucellar tissue are frequently small, deeply stained in safranin, and apparently going to pieces. In one case at about this stage the nuclei in this position had entirely disappeared for a distance of several layers beyond the normal large-celled tissue. *Fig. 47* shows the large-celled tissue at a later stage. It has increased greatly in amount and the cells, which are now slightly separated from each other, are much more numerous. They retain the characters mentioned above for a younger stage.

The nucellar cells bordering on this tissue now show unmistakable signs of disorganization. They are completely crushed and broken up and are as strongly distinct from the large-celled

tissue as the latter is from the megaspore. *Fig. 48* is a more magnified section of the same spore and tissue. A small amount of granular material appears between the spore and the large-celled tissue, but the inner walls of the latter are apparently intact. A few cases were found, however, where the innermost of the large cells seemed to be partly broken up on the side next the spore. At the stage shown in *fig. 49* the existence of so definite a layer around the spore is doubtful. The cells adjoining the spore are still larger than others beyond them, but in all cases that I have found they are more or less separated from each other and approach in appearance the loosened "spongy tissue" which has been described in other cases. In later stages, however, there constantly occurs a single layer of very large rectangular cells lying next to the megaspore, while beyond those the ordinary nucellus-tissue is crushed and disorganized. *Fig. 51* shows such a layer around a large spore before the formation of the cellular prothallium. The large cells seem perfectly intact; walls are present on both sides and the nucleus is large, has an abundant reticulum, and is more like what would be expected in an actively secreting cell than in a rapidly disorganizing one. *Figs. 52* and *53* show the same layer at a later stage, just before the prothallium has reached its full size. In *fig. 52* the wall of the megaspore has shrunken somewhat and the large cells have become more elongated and slightly separated. The layer of large cells and two or three layers of ordinary cells beyond it are always furnished with starch during the growth of the prothallium; the starch is continually accumulating in the further-removed cells as the inner ones are being disorganized. The large-celled layer is also destroyed at the last moment and the mature prothallium is surrounded at its upper end with four or five layers of ordinary nucellar cells. In the Abieteae the young germinating megaspore is imbedded in a loose tissue which resembles somewhat the large-celled tissue just described in Taxodium. Its limits are so distinct that Hofmeister ('62) mistook it for endosperm. In comparing Strasburger's ('79) figures of such tissue in Pinus and Larix with my *figs. 45* and *47* in Taxodium, it will be seen

that there is a great difference in structure in the two cases. Moreover, this tissue in the Abieteae is always spoken of as disorganizing. Coulter and Chamberlain ('01) have an interesting paragraph on this subject. They say: "In our figure of a mother-cell of *Pinus Laricio* imbedded in nucellar tissue, it is apparent that it is surrounded by a rather definite zone of cells, two to four layers in depth, which give evidence of breaking down. After endosperm-formation is somewhat advanced, this interesting zone becomes differentiated into two distinct regions, an outer layer of tabular, almost empty, cells, and an inner region of polygonal cells with densely staining contents." I do not know of any case, however, where this layer is said to persist in later stages. Strasburger ('79) describes a zone of more or less disorganized cells around the germinating megaspore of Thuja. I have examined growing sacs of Pinus, Larix, Thuja, Podocarpus, and Taxus in reference to this point. At the base of the prothallium in Podocarpus and around the very young germinating megaspore of Thuja there are cells which approach, in appearance, those found in Taxodium. In fact, there are frequently present around growing prothallia a number of swollen free cells, which might be compared to such a tissue as I have described in Taxodium, but in most cases these cells are not in close contact with one another and their development can be gradually traced from the ordinary cells of the nucellus. But I have not studied any of these plants carefully enough to deny the persistence in them of this tissue, and further observation is necessary to decide the matter.

It is difficult to understand the constant occurrence of a definite layer of large, distinctive, undisorganized cells around the growing prothallium in Taxodium, unless we ascribe to them an active part in the nourishment of the young gametophyte, and this I believe to be their real function. If this interpretation is the correct one, the tissue in question may be considered as a tapetum, which, instead of disorganizing at the maturity of the spore, as is usually the case, has continued its growth to keep pace with the developing prothallium which it continues to nourish until mature. If we consider the archesporium as

reduced to a single cell (the megaspore mother-cell), the tissue immediately around this cell must be considered as a tapetum, and we have seen that it is probably by the division of this tissue that the nourishing layer is formed. This cannot as yet be positively asserted for the later stages, as all steps have not been followed. The only other interpretation that seems possible is that the cells immediately surrounding the megaspore represent an originally archesporial tissue which has given up its function of spore-production and taken up the new rôle of nourishing the young plant within. Of these two interpretations I consider the first as much the more likely.

It is well known that the tapetum in the megasporangium of Selaginella persists intact until some time after the sprouting of the spores, which in this case are shed only after a considerable growth has occurred. Should the spores not be shed at all, and the tapetum continue still further its growth and function, we would have a condition paralleling that found in Taxodium.

DEVELOPMENT OF THE PROTHALLIUM.

We have left the megaspore to follow the surrounding tissue through its subsequent stages. The growth of the germinating megaspore is extremely slow during the first month after its formation, having reached on April 29 only about the 32-celled stage (*fig. 47*). Growth now becomes more rapid, and on May 6 it has reached the stage shown in *fig. 49*. About the beginning of June growth has stopped in the upper part and the formation of cell walls begins. *Fig. 25* shows a stage just before the beginning of cell-formation. The pollen tube has already reached the megaspore, which now contains an enormous vacuole surrounded by a protoplasmic layer containing nuclei. In this case the protoplasmic layer has collapsed.

The great size reached by the germinating megaspore before the formation of cellular tissue seems to distinguish Taxodium from other conifers thus far studied. The wall of the spore was found to be furnished with pits. *Figs. 97* and *98* show those pits in surface view at a time shortly before the formation of a cellular prothallium. The manner of the formation of the

first cell walls in the young gametophyte is shown in *fig. 24*, and I can confirm Mlle. Sokolowa's observation, also recently repeated by Ikeno ('98) and Arnoldi ('00), that the inner sides of the first cells are open. Mlle. Sokolowa gives the name "alveoli" to the ingrowing tubular cells of the prothallium, but this term does not seem to have much to recommend it. It is repeated by Arnoldi ('00) in his work on Sequoia.

In view of the supposed relationship of Taxodium and Sequoia, it is of interest to compare the endosperm-formation in the two cases. Arnoldi has described in some detail a double process in Sequoia which he considers to have significance from the phylogenetic point of view. The prothallial region which is to bear the archegonia is formed in the usual way by ingrowing open tubes, which finally meet in the center. This area may be either in the center of the sac alone, or may extend entirely to the tip. In the latter case, however, Arnoldi considers the tip to be lacking. The tissue at the tip does not form in the usual way, but it is produced by free cell-formation, as in the endosperm of angiosperms. This free cell-formation begins in the tips before the tubes appear in the archegonial region. In Taxodium, on the contrary, cell-formation usually begins earlier at the tip, where archegonia are to appear, than at the base of the prothallium, and firm cell walls are frequently lacking in the lower parts long after they have been established in the upper. In fact, cases are not infrequent in which the lower part of the gametophyte is in an embryonic condition, even after fertilization has occurred in the archegonia. In some cases, however, firm cell walls seem to be formed almost simultaneously throughout the spore. In the upper part of the prothallium it is always easy to see that cell-formation has proceeded by the usual growing-in method.

Fig. 55 shows prothallial tubes from near the tip of the sac after their closure on the inner side. (Mlle. Sokolowa ['90] has shown that the closure occurs when the inner ends of the tubes meet in the center.) *Fig. 56* shows the first division of a prothallial tube and the preparation for the second. By these divisions there are formed rows of cells radiating from the

center outward. *Fig. 57* represents the whole tip of a prothallium at the same stage as in *fig. 56*. Mlle. Sokolowa describes the nucleus of the open prothallial tube as remaining at the inner end during its growth toward the center, but after the formation of the closing walls the nucleus again moves back to near the periphery of the cell. From *fig. 54* we see that the first statement is true in Taxodium, at least during the very young stages. Good preparations were not obtained by me in older prothallial tubes before the closure. From Mlle. Sokolowa's figure of Juniperus, it seems that the mother-cells of the archegonia behave in this respect just as the other cells of the prothallium, and this is probably true in Taxodium also.

The prothallial formation in the lower part of the spore does not appear to me to be different in essentials from its formation above. It is only in the late development of cell walls, and not in their peculiar origin, that the difference consists. The lower part, even after the formation of cell walls, continues to increase in size long after the upper part has ceased to grow. In the ripe seed the upper end of the nucellus is no larger than at the time of fertilization, while the lower part increases greatly in size, the whole prothallium acquiring the shape of a slightly bent club. After a certain number of cell walls are formed in the prothallial tubes, nuclear divisions occur without the formation of cell walls, and there arises a multinucleate condition (*figs. 58, 59*). These nuclear divisions are generally, at least, of the mitotic type. Jäger ('99) describes a fusion of nuclei in the prothallial cells of Taxus, but I have not found the number of nuclei appreciably smaller in Taxodium even after the formation of the embryo.

DEVELOPMENT OF THE ARCHEGONIA.

The archegonia of Taxodium are disposed exactly as in the Cupresseae. They form a compact group at the base of a common depression in the center of the tip of the prothallium. Among the many hundred prothallia sectioned only three or four were found in which any variation in this arrangement occurred. In these exceptional cases there were several smaller

groups of archegonia which were separated by a few layers of prothallial cells. They were always situated at the tip of the prothallium, but sometimes faced to one side.

In *fig. 57* the initial cells of the archegonia are shown just before the cutting off of the neck cell. The nucleus is situated at the very tip of the cell and most of the protoplasm is collected around it. A very large vacuole occupies the greater part of the archegonium. In *fig. 60* the neck cell is being cut off. The nuclei in the central initials are preparing to divide. Their nucleoli are fragmented, and although this nuclear division was not followed in detail, the indications are that it is essentially like that in which the ventral canal nucleus is cut off. *Fig. 61* shows the neck divided once longitudinally. In *fig. 62* the neck cells are densely filled with starch and the amount of protoplasm in the central cell has increased greatly, especially in the lower part. In the occurrence of a single large central vacuole in the archegonium Taxodium resembles the Cupresseae and differs from all other conifers so far studied. At this stage we first notice slightly denser areas in the protoplasm at each end. The upper lies very near the nucleus and is smaller than the lower, which occupies a central position in the accumulated basal protoplasm. The nucleus of the central cell at this stage is very like that of the prothallial cells around it. In *fig. 68* there has already appeared around the archegonial group a distinct layer of sheath or jacket cells. At the basal end of the group the angles between the archegonia are filled by these jacket cells, which are at this point generally larger than on the sides. This jacket is a constant accompaniment of the archegonia in all gymnosperms with the exception of Welwitschia. Arnoldi ('00) reports that in Sequoia the layer is incomplete, only certain cells acquiring the distinctive characteristics of modified jacket cells. I have frequently found in Taxodium a cell within this sheath, which in its poverty of contents was easily to be distinguished from its neighbors, and resembles closely the ordinary prothallial cells around it. By far the larger number of the cells directly adjoining the archegonia, however, are modified in the usual way into the nourishing jacket cells. The nucleus of the central cell, at

the stage in *fig. 62*, is larger than the cells of adjoining tissue, but does not differ from them in structure. There is an abundant peripheral reticulum, staining blue throughout with gentian violet, and a nucleolus of compound structure, such as was found in the initial cell nucleus. In place of the single nucleolus there is frequently present a central group of quite distinct granules (*fig. 63*). All stages can be found between the distinct granules and the single compound structure formed by their fusion. From the nucleolus, or from the separate granules, linin threads extend which place the nucleolar matter in direct connection with the reticulum of the nucleus, and this I believe to be a constant character in nucleoli of chromatin material. That this nucleolus is largely composed of chromatin is shown by its subsequent behavior. As already mentioned, the nucleolar structure is the same in the prothallial cells and jacket cells, with the exception that in these the central or nucleolar collection of chromatin is quite inconstant in amount, the size of the nucleolus varying in proportion as the red-staining granules of the reticulum are more or less abundant.

The number of archegonia in a group varies greatly. *Fig. 64* shows a longitudinal section through a group of at least thirty-four archegonia, ten appearing in a single section. This is a larger number than has been found in any other gymnosperm, with the exception of Sequoia. The number is generally from ten to twenty, but in poorly developed prothallia there may be only a half dozen or less. *Fig. 65* is a cross section of a group of seventeen archegonia.

The neck cell very soon after its formation divides by a longitudinal wall into two cells of about equal size. This division is followed usually by another in each cell at right angles to the first, to form a tier of four cells (*fig. 94*). If the neck of the archegonium is crowded or flattened, the second division may occur in one or both of the two first-formed cells (*fig. 93*). As the archegonium reaches maturity, the nuclei of the neck cells generally divide again, and walls may or may not be formed succeeding this division. The walls when formed are very irregular in position. They are frequently somewhat inclined and

may or may not intersect the outer wall of the cell. In this way outer and inner cells are frequently formed (*fig. 66*), but two distinct tiers extending across the neck are never present. *Figs. 66, 93, 96* show the diversity that may occur in the neck. The cells are of unequal size and the number may vary from two to sixteen or even more. Very soon after their last division the neck cells begin to disorganize. They contain starch until the beginning of their disorganization, which takes place somewhat sooner here than in the jacket cells. *Fig. 66* shows an archegonium in which this disorganization is proceeding. There are present at the tip of the protoplasm of the central cell a number of bodies staining deep red with safranin, which may easily be mistaken for fragments of a disorganizing ventral canal nucleus. The last division, however, has not occurred in the central cell, and these bodies are probably the transferred remains of the broken-up nuclei of the neck cells. They are the first such bodies to appear in the archegonium, and in this stage are very conspicuous as a cap at its tip. This early transfer of nutrient material from the neck cells is probably explained by the advantage to be gained in having this transfer completed before fertilization has disturbed the relations between neck and central cell.

The jacket cells around the archegonia generally contain two nuclei each at this time (*figs. 67–69*), but this condition may be reached sooner. About the time that the ventral canal nucleus is cut off, the nuclei of the jacket cells begin to disorganize in the way already described in Cycas by Ikeno ('98) and in Ceratozamia by Arnoldi ('00). The network and the nucleoli resolve themselves into a number of deeply staining bodies, which by the disorganization of the nuclear walls come to lie free in the cytoplasm (*figs. 71–74*).

Immediately before fertilization there begin to appear in the cytoplasm of the egg the proteid vacuoles described in species of Abieteae. Such vacuoles are shown in *fig. 75* and have the same structure that has been described in other cases, but they are not very conspicuous or abundant in Taxodium. Arnoldi ('00) believes these vacuoles to originate in some cases from the

nuclei of the sheath cells of the archegonium, and thinks he has traced their entrance through protoplasmic connections in several species of Pinus and in *Abies sibirica*. From his work on Dammara and Cephalotaxus he is inclined to consider their origin as the same in these cases also. While I have not been able to establish the existence of protoplasmic connections between egg and sheath cells, the appearance in *fig. 83* strongly suggests that such connections exist, and the presence of pits in the wall of the archegonium would also imply their occurrence.

The two denser areas already noticed in the very young archegonium (*fig. 62*) have reached in *fig. 63* a size and condition retained until the initial changes which bring on the division into the central canal and egg nuclei. These areas are of dense fibrous material, and are by far the most striking features in the archegonium of Taxodium. They stain much more deeply with orange G than does the surrounding cytoplasm, and from them fibers radiate to the surface of the cell. It will be noticed that the denser part is at the periphery of the mass, but the inner part is also denser than the ordinary cytoplasm of the cell, and the whole is composed of a complex of granular fibers. The upper of these masses is the smaller and lies very near the nucleus. Fibers can be traced passing from the central mass around the nuclear wall, and they seem to be a continuation of the wall itself. That these bodies are of the same nature as the so-called kinoplasmic material, generally most conspicuous at the time of nuclear division, is evident. They show the same structure as the much less developed kinoplasmic areas already mentioned in the megaspore. Such bodies have not heretofore been described as occurring in such perfection in any case with which I am acquainted. Kinoplasmic areas have been mentioned near the nucleus at the time of its division in the archegonium of *Tsuga canadensis* by Murrill ('00), and Ikeno ('98) has figured such areas under the central cell nucleus of Cycas. Chamberlain ('99) gives one case where there are two such bodies near the egg nucleus in *Pinus Laricio*, and Blackman ('98) describes fibers of this nature radiating from the egg nucleus before fertilization. In all these cases, however, the fibrous material is not nearly so

conspicuous as in Taxodium, and in no case has a second kinoplasmic body been noticed in the lower part of the archegonium. Just before the central cell nucleus prepares to divide the kinoplasmic bodies undergo a marked change. They increase greatly in size, the central part becoming thinner, until finally the denser material, which has by this time become confined to a peripheral position, is broken up into more or less separate groups. In the upper end, one of these groups lying nearest the nucleus becomes most conspicuous, while the others become less and less distinct, their fibers finally arranging themselves into the immense aster which radiates from the inner side of the nucleus. Fibers extend around the nucleus from the center of the aster and merge insensibly into the nuclear wall (*fig. 78*). The lower kinoplasmic mass has also become broken up into separate parts, forming an incomplete ring, and during the activities in the upper part connected with the cutting off of the ventral canal nucleus these separated groups below become likewise extremely active and fill the whole base of the archegonium with conspicuous figures of various shapes, such as fans, asters, double asters, test-tube cleaners, etc. In fact the whole kinoplasmic content of the archegonium seems as if electrified. A few of these structures are shown in *figs. 90–92*.

Chamberlain ('99) figures such radiations in the egg of *Pinus Laricio* after the formation of the ventral canal nucleus, and considers them as parts of the enormously developed spindle of that division. In Taxodium, however, the kinoplasmic radiations in the lower part of the archegonium are in no way connected with the spindle above, although they are most active at the time of its formation. The function of these kinoplasmic masses is obscure, and I can suggest no explanation unless it be that the great length of the archegonia in Taxodium and the fact that it is principally at the end farthest away from the nucleus that they are exposed to the sheath cells may make it advantageous to have a more definite mechanism for the regulation of the entrance of the plastic material at this end.

[*To be concluded.*]

MITOSIS IN PELLIA.[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY, XLIX.

CHARLES J. CHAMBERLAIN.

(WITH PLATES XII–XIV)

JUST as an understanding of the gametophytes of the flowering plants has been gained by a comparative study of the progressive reduction of the gametophytes of the higher cryptogams, so, in our opinion, the processes of nuclear and cell division in the flowering plants will be understood only after an investigation of these processes in lower forms; and just as the pteridophytes show the transitions which have cleared up the homologies of the gametophytes, so, it seems probable, the Hepaticae, in their modes of mitosis, show the transitions which will lead to a correct interpretation of mitotic phenomena in the flowering plants. The Hepaticae, however, have received comparatively little attention from cytologists.

In 1893, Schottlander (30)[2] described the sexual cells of several liverworts, paying particular attention to spermatogenesis. In the antheridia of Marchantia he found that the centrosomes divide during the anaphases of mitosis, so that each daughter-nucleus is accompanied by two centrosomes; but in the egg, centrosomes were not identified positively.

In 1894 Farmer (8) reported a quadripolar spindle in spore mother-cells of Pallavicinia. According to this account, the chromatin of the spore mother-cell breaks up into sixteen chromosomes, four of which are then conveyed simultaneously to each of the four spores. In the same year Farmer (9), in collaboration with Reeves, described centrospheres in the germinating spores of Pellia. In the following year Farmer (10)

[1] Published concurrently in the Decennial Publications of the University of Chicago 10:327–345. 1903.

[2] Figures in parentheses refer to literature cited at the end of the article.

published a more extended paper dealing with spore-formation and nuclear division in Fossombronia, Pellia, Conocephalus, and several other forms. In most of these forms, centrosomes were observed to play an important rôle in mitosis. The occurrence of centrosomes in Pellia was confirmed by Strasburger (**33**) from Farmer's own preparations.

In 1899 Davis (**6**) studied the spore mother-cell of Anthoceros. In the two divisions by which the tetrad is formed from the mother-cell, the spindle during the metaphase is flattened at the poles and entirely lacks bodies which might be interpreted as centrosomes or centrospheres. The spore walls are described as being formed independently of the spindle.

The following year Van Hook (**38**), with more favorable material, confirmed Davis's statement that there are no centrosomes in the spore mother-cells of Anthoceros, but found the spindle functioning as in Lilium in the formation of spore walls. In the same paper Van Hook figured and described definite centrosomes in the vegetative cells of the gametophyte of Marchantia.

In 1901 Davis (**7**) made a detailed study of mitosis in various phases of the life-history of Pellia. Centrospheres were found during the early divisions in the germinating spore, but could not be identified in the sporophyte or in later stages of the development of the gametophyte.

At this time it hardly seems desirable to make a more extended résumé of the literature, since it is still too incomplete and indefinite to warrant generalizations. In presenting our own results, we shall occasionally refer to the preceding papers and also to papers dealing with mitosis in other groups.

MATERIAL AND METHODS.

Most of the material for this work was collected near Bonn in Melbthal and in the Siebengebirge. Early in October the spore mother-cells of Pellia are already quite deeply lobed, and occasionally a sporogonium is found in which the spores are already formed. By the middle of November nearly all of the spore mother-cells have divided and many of the spores have germinated. The winter of 1901–2, in the Rhine Province, was a

very mild one, and germination proceeded with only occasional interruption throughout the entire season. Material brought into the laboratory at any time after the middle of November developed much more rapidly than in the open, and would shed the spores within a week or ten days.

Before placing the material in the fixing agents, the calyptra was dissected away and about one-third of the sporogonium cut off with a razor, thus freely exposing the spores. In a few cases the mass of spores, held together only by the elaters, was removed from the sporogonium, but while not nearly so many spores were lost as might be anticipated, this tedious method was found to be unnecessary, since the other process readily yielded smooth sections as thin as 2 or 3 μ.

Several fixing agents were used, but only two gave thoroughly satisfactory results. These were chrom-acetic acid (0.8^{gm} chromic acid, 0.5^{cc} glacial acetic acid, 100^{cc} water) and a modification of Flemming's solution (0.5^{gm} chromic acid, 0.5^{gm} glacial acetic acid, 1 per cent. osmic acid 10^{cc}, water 100^{cc}). While achromatic structures stain more readily after solutions containing some osmic acid, equally good preparations were often obtained from material fixed in the former solution.

Most of the sections were cut at 2 or 3 μ, but sections 5 μ, and even 10 or 15 μ in thickness, were used in determining the number of asters and in counting chromosomes.

Haidenhain's iron alum haematoxylin, with or without a slight tinge of erythrosin, Congo red, or orange G, gave fairly satisfactory preparations, but gentian violet proved to be so much superior in differentiating kinoplasmic structures that safranin and gentian violet, sometimes with the addition of orange G, were used in most of the work. Sections were stained, usually over night, in safranin (1^{gm} safranin in 100^{cc} of 50 per cent. alcohol), then washed in 50 per cent. alcohol until all red color was removed from the achromatic structures, and then stained for one or two hours in gentian violet (saturated aqueous solution). From the gentian violet the preparations were transformed directly to absolute alcohol, where they were quickly dehydrated, the process being hastened by moving the slide to

and fro in the alcohol. Clove oil was used for clearing. The clove oil should be rinsed off with good cedar oil, otherwise the gentian violet gradually fades. When orange G was used the preparations were taken from the gentian violet, dipped a few times in water, stained for one minute in orange, and then transferred to the absolute alcohol.

In studying the preparations glass globes, filled with various solutions, served as ray filters and condensers. A light blue solution of ammoniated copper sulfate was used for most of the work, but occasionally a light violet solution of permanganate of potash, imitating the gentian violet stain, gave a sharper differentiation of the kinoplasmic structures.

While the work deals chiefly with the first three divisions of the germinating spore of *Pellia epiphylla*, and in these divisions is largely confined to the centrospheres, asters, and spindle, mitosis was studied in other phases of the life-history of this genus, and also in several other liverworts, among which were Conocephalus, Marchantia, Aneura, Pallavicinia, Scapania, Lophocolea, and Porella.

The principal results of the investigation were presented in a *Vortrag* before Professor Strasburger and the advanced students of the Bonn laboratory in February 1902, and in July of the same year a brief résumé was presented before the botanical section of the American Association for the advancement of Science.

THE SPORE MOTHER-CELL.

The spore mother-cell was observed in *Pellia epiphylla*, *P. calycina*, *Aneura multifida*, and in *Porella platyphylla*. In all of these forms the nucleus occupies a central position during the development of the lobes which are to become spores. It seems probable that the nucleus is concerned in the formation of the lobes. We found nothing to support Davis's (7) statement that the nucleus lies in one of the lobes until shortly before the first division of the mother-cell. No quadripolar spindles, like that described by Farmer (7) for Pallavicinia, were found in any of the above-mentioned forms. On the contrary, the four spores in all these cases are formed by two successive divisions, as described by Farmer (10)

and by Davis (7) for *Pellia epiphylla*. Unfortunately, no material of Pallavicinia in this stage was available, but the striking resemblance of Farmer's (8) figures to the mitoses in deeply lobed mother-cells of other Jungermanniales leads us to suggest, as Davis (7) has already done, that Farmer (8) may have misinterpreted the quadripolar figure in this genus.

THE GERMINATING SPORE.

The first, second, and third mitoses in the germinating spore of Pellia cannot be regarded as distinct types, for with diligent searching one could select a series of mitoses at the second division, or even at the third, which would be identical with a series at the first division. In fact, we have used *figs. 7, 8*, and *19* of the third mitosis to illustrate also the same stages in the first and second mitoses. Nevertheless, it is true that, in a great majority of cases, kinoplasmic activity is most energetic during the first division, and that in succeeding divisions it becomes less and less conspicuous, until centrospheres and asters cease to attract any attention, and it finally becomes doubtful whether they are present.

THE FIRST MITOSIS IN THE GERMINATING SPORE.

As the nucleus of the germinating spore increases in size preparatory to the first division, the area immediately surrounding it becomes comparatively free from starch grains and coarser granules (*plate XII, fig. 1*). It seems reasonable to suggest that some substance, escaping from the nucleus into the cytoplasm, causes this zone and acts as a stimulus to the formation of the extra-nuclear portions of the achromatic figure. It is not impossible that such a substance might actually take the form of a centrosphere. (The origin of the aster will be considered when dealing with the second division.) After the spirem has become segmented into chromosomes the nucleus elongates and the nucleolus appears very much vacuolated (*fig. 2*). At this stage a pair of dome-shaped caps (*figs. 3, 4*) may be recognized at opposite poles of the nucleus. These caps, which will be considered later, appear in transverse section as a delicate ring, but a similar section of the completed spindle shows a dense mass of fibers (*fig. 5*).

During the early prophases the poles of the spindle are usually rounded (*figs. 3, 4, 6*), but, as the metaphase approaches, the caps (*figs. 3, 4*) which have given the poles of the spindle a rounded form become resolved into fibers, and the poles may vary in shape from sharply-pointed figures, like that shown in *fig. 10*, to such broad, indefinite ones as those shown in *figs. 8* and *27*. Spindles with three and even more poles are not very rare. They do not originate like the multipolar spindles of the spore mother-cells of vascular plants, but are preceded by the bipolar condition or are formed through the influence of three or more centrospheres or asters (*figs. 16, 23*). During the anaphases the poles of the spindle are sometimes sharp and sometimes indefinite.

In the prophases it is plain that the achromatic figure is made up of the asters and two half-spindles (*fig. 6*). As the spindle continues to develop, some of the fibers—the mantle fibers—become attached to the chromosomes; the other fibers increase in length until they reach the opposite pole, thus forming a part of the central spindle.

While the poles are separated from each other, radiations are easily seen, and they continue to be fairly conspicuous until the spindle has reached its full length, when they rapidly disappear, losing their staining capacity first at the peripheral ends, then throughout their entire length, and finally becoming indistinguishable. When the metaphase is reached, the radiations have usually disappeared (*fig. 7*), and during the anaphases, while the chromosomes are passing to the poles, it is very seldom that any trace of radiations can be found. In the telophases, however, the radiations reappear, but are not centered in any single point. When the nuclear membrane begins to form, the radiations again become indistinct and disappear as before. Just before the spindle reaches its full length (*fig. 6*) the radiations often attain their greatest prominence, sometimes appearing as extremely coarse strands. In nearly all cases, even in very thin sections, some of the rays can be traced from the pole of the spindle to the *Hautschicht*. The diameter of the rays is usually greater at the polar end, but a slight increase in diameter at the *Hautschicht*

also is not uncommon. The rays are usually simple, but may be branched especially during the earlier stages.

It is worthy of note that the radiations are most pronounced and stain most deeply with gentian violet, while the nucleus is elongating and its poles are separating from each other; and, further, that during this period many of the radiations connect the poles with the *Hautschicht.* The explanation which we venture to suggest is that the radiations take an active part in separating the poles from each other. The fact that the radiations disappear as soon as the poles have reached their widest separation supports this hypothesis. The reappearance of the rays in the telophase does not seem to be so definitely concerned with movement, because they again disappear before the nucleus has perceptibly changed its position: still, it is possible that there may be a slight movement in the nucleus toward the center of the new cell. The reappearance, however, takes place as the nuclear membrane begins to be formed, and it may be an expression of kinoplasmic activity during the formation of the *Hautschicht* surrounding the nuclear membrane, or the rays may be contributing to the formation of the nuclear membrane itself, which, we believe, is largely kinoplasmic in its nature.

THE SECOND MITOSIS IN THE GERMINATING SPORE, WITH REMARKS ON APICAL CELL, ANTHERIDIA, NUCLEOLI, AND CHROMOSOMES.

The second mitosis is remarkably easy to fix and stain; so that, while the first mitosis, if equally well prepared, might show the early prophases with a little more clearness, our material afforded a better study of these stages during the second mitosis.

In studying the second mitosis, special attention was devoted to the centrosphere and to the origin of the achromatic structures. The terms "centrosome" and "centrosphere" are frequently confused. Until much more is known about the origin of these structures and their relation to each other, it is hardly worth while to attempt any definitions. A typical centrosphere —as the term is used in this paper—is shown in *fig. 12.* The centrosphere consists of the same substance as the astral rays and the spindle fibers. The elongated body toward which the

rays converge in *fig. 15* is also a centrosphere, and the densely staining masses at the poles of the spindle in *fig. 6*, although not organized into a definite body, consist of the same material as centrospheres and, at an earlier stage in mitosis, may have had a more definite form. We have not intended to represent a *centrosome* in any of our figures. Bodies which have the superficial aspect of centrosomes are shown in *figs. 14, 16*, and *17*, but here the sharply staining body at the center of the centrosphere is, without doubt, the cut end of an astral ray. The structure at the upper pole in *fig. 9* certainly looks like a centrosphere containing a centrosome, but such an appearance is so rare that it seems safer to regard the sharply staining body as a chance granule. Still, it is evidently just such a body as this that Van Hook (**38**), in his recent study of Marchantia, interprets as a centrosome.

In the very early prophases a beautiful system of radiations becomes quite conspicuous. This system we regard as an aster, comparable with the asters of thallophytes and of animals. The system first appears as a few fibers converging to a point which is usually in contact with the nuclear membrane or very near to it (*figs. 11–13*), but, in some instances, may be at a considerable distance from the nucleus (*figs. 14–16*). Persistent search failed to reveal any body which could be identified positively as a centrosome or centrosphere before the appearance of the aster, and even after the appearance of the aster and centrosphere, no centrosome could be distinguished. Granules, like those shown in all the figures, were frequently found in contact with the nuclear membrane after the nucleus had begun to enlarge, and it is probable that some of the granules were centrospheres, although no method was found for identifying them before the appearance of the rays. Bodies which bear remarkable resemblance to centrosomes (*figs. 14, 16, 17*) and which. for a time, were interpreted as genuine centrosomes, proved to be merely the cut ends of coarse fibers. Sometimes several deeply staining points may be seen; such an appearance might easily be mistaken for a centrosphere containing several granules. In cases like those shown in *figs. 14–17*, the "granules"

are, without doubt, nothing but the cut ends of fibers. The two centrospheres in *fig. 17* are practically alike, but the one at the upper pole is represented in median section and the other in surface view, the fibers in vertical view appearing as dots. How ever, it must be admitted that occasionally the deeply staining points are really granules (*fig. 9*), but the cases are so rare that we have not regarded such granules as a functional part of the mitotic mechanism.

After a study of the germinating spore had failed to show any centrosomes, the nuclear figures were examined in other phases of the life-history, particularly in the apical cell and its younger segments, and in the developing antheridia. The apical cell and the rapidly dividing cells near it are quite favorable for study. The character of the mitoses in this region is represented in *figs. 9* and *10*. The lower pole in *fig. 9* shows the more usual condition, although the rays are frequently as strongly developed as those shown at the upper pole, a considerable number of the rays reaching to the *Hautschicht*. A careful examination of this figure will show that there is no definite centrosphere like those in *figs. 12* and *13*. In later stages (*fig. 10*) the spindle becomes sharply bipolar and the radiations disappear.

The antheridia were examined with particular interest because Schottländer (**30**) had reported centrosomes during all stages in the development of the antheridium of Marchantia, and Belajeff (**2**) had found blepharoplasts throughout the development of the spermatogenous cells of Marsilea. However, nothing which could be interpreted as a centrosome was found in our material, which furnished a series from the initial cell up to stages in which more than thirty cells appear in a transverse section of the antheridium. Unfortunately, the material showing the last two or three divisions preceding the formation of the spermatozoid mother-cells was not satisfactory, and, consequently, no positive statement can be made in regard to blepharoplasts, although we should assume them to be present during the last one or two mitoses.

In the germinating spore a differentiated area, already

described as a centrosphere by Farmer (9), Strasburger (33), and by Davis (7), is often found at the center of the aster. The origin and behavior of this structure, which we regard as a genuine centrosphere, are rather puzzling. While we assumed that it must appear earlier than the rays, and that the rays were developed from it, the failure to identify the structure before the appearance of the rays, and its frequent absence when it might be expected to be present, led to a careful study of the subject. The conclusion was reached that the centrosphere gives rise to the rays, but that the rays may also contribute materially to the substance of the centrosphere.

Although we have not been able to make any satisfactory study of living material, we believe that appearances warrant the theory that there is a streaming movement in the rays. Such a theory is not entirely new to zoologists. If the theory be true, when the streaming is toward the nucleus the centrosphere would increase in size, while a continued streaming toward the periphery would cause the centrosphere to disappear. In regard to the origin of the rays, nothing more definite was determined. Finely granular areas, showing a tendency to stain with gentian violet, were sometimes seen in earlier stages, but the actual formation of rays or centrospheres from these areas could only be surmised. These areas do not seem to differ essentially from those which we (4) have already observed accompanying the male nuclei of *Pinus Laricio*. In some of Miss Ferguson's (13) figures of the same species and of *Pinus rigida* the areas approach the form of definite centrospheres. The aster appears so suddenly that its mode of development is largely conjectural. In a fully developed aster there is usually an increase in the diameter of the ray at the centrosphere (*figs. 13* and *16*), and occasionally a slight enlargement at the *Hautschicht*. An enlargement of the ends of the rays, as shown in *fig. 13*, is just what should be expected if there is a streaming of material. The variability in the size of the rays and their irregularly granular character also favor the theory that they are lines of streaming material. The tendency of small nucleoli or microsomes to collect on the rays, as pointed out by Schaffner (27) in his study

of Lilium, and as is familiar to all who have seen mitoses in the embryo-sac of Lilium and similar forms, is another argument in favor of this theory.

The asters arise at opposite poles of the nucleus, but not simultaneously. Serial sections of a large number of nuclei were examined before this conclusion was reached. We can hardly understand Davis's (**7**) statement that in his studies he "has never found a nucleus with a clearly defined solitary aster beside it. This is a very important point and the search was persistent." In our own preparations of the second and third mitosis we never found anything but the solitary aster in the earliest stages. In studying this point, reconstructions were made from thin sections, and series were cut thick enough to include the entire nucleus. It is true that the first aster does not usually reach its fullest development before one appears at the opposite pole. In *figs. 14* and *15* and also in *fig. 19* (third division) there is only one aster. However, the second aster usually appears before development has proceeded so far. In spite of the fact that the two asters do not arise simultaneously we can confidently support Davis's (**7**) conclusion that the two asters do not arise by the division of a single one. We found only two preparations in which the asters were less than 180° apart, except in case of tripolar figures, which were not very rare (*figs. 16*—third pole not shown—and *23*). In early stages the two poles usually differ from each other in appearance, one pole being rather pointed and the other comparatively blunt (*figs. 21, 22, 24, 25*). Cases like *fig. 21* indicate that the blunt pole has been the last to develop. At this stage, neither pole is sharp, both being more or less rounded. The dome-shaped prominences or "caps," as they may be called, are by no means easy to interpret. In some cases the cap looks like a mere extrusion of the nuclear membrane, while in others the nuclear membrane is still intact after the caps have become quite conspicuous. The rounded ends indicate considerable pressure from beneath. That the cap is something more than a structure built up by fibers radiating from the aster is shown by its appearance and by the fact that in transverse section it presents a continuous line. The cap becomes

finely granular and suggests a delicate membrane being resolved into fibers, rather than a membrane being formed from fibers (*fig. 4*). In our opinion the cap is a delicate layer—a sort of *Hautschicht*—immediately surrounding the nuclear membrane. Were it not for the fact that the nucleus retains its form and seems to be surrounded by a membrane even after the caps have become quite conspicuous, we should conclude that the cap is only the distended nuclear membrane. At first the space between the cap and the surface of the nucleus is filled with a fluid in which no fibers or granules can be detected, but later, after the nuclear membrane has broken down, a dense mass of spindle fibers appears and occupies the space between the two caps. The caps do not seem to be different from those seen in the root tips, as described by Němec (**24**), Schaffner (**28**), and others.

The rays of the aster do not penetrate the caps, but are closely applied to them. The aster exerts a strong pull, as may be seen during the period of elongation, although the elongation is due, in some degree, to pressure from within.

As in the first mitosis, the spindle in early stages consists of two half-spindles (*fig. 26*). Until the caps become resolved into fibers they keep the spindle rounded (*fig. 26*). The caps generally break up into fibers during the metaphase or early anaphases, and the poles of the spindle may then become blunt or irregular (*fig. 27*). Occasionally the caps keep the poles of the spindle rounded even after rather late anaphases have been reached (*fig. 28*).

The polar radiations generally disappear at the end of the prophases, are absent during the metaphase and anaphases, and reappear in the telophase (*figs. 26–29*). That portion of the spindle which lies between the two caps is undoubtedly nuclear in origin. It consists of a very dense mass of spindle fibers which appear with remarkable suddenness (*fig. 20; cf. fig. 5*).

From observations on the nucleolus, we feel sure that this body contributes considerable substance to the growing chromosomes. As the chromosomes increase in size, the nucleoli become more and more vacuolated, and material which resembles that of the nucleoli is often found adhering to the growing chromosomes.

After the chromosomes have reached their full size, the nucleoli fragment, the fragments usually staining with gentian-violet. Soon the entire nuclear cavity becomes filled with granular matter staining with gentian-violet, and at this period the central portions of the spindle appear suddenly as the granular matter disappears. A few early spindles were noted in which this central portion did not seem to consist of sharply defined fibers. While such an appearance is often due to faulty methods, the sharply defined fibers in other figures in the same preparation favor the inference that these undifferentiated portions represent stages in the transformation of nucleolar matter into spindle fibers. In our opinion, these phenomena support Strasburger's (33) theory that the nucleolus contributes some of the material for the spindle.

Observations on the chromatin were merely incidental, but it is certainly safe to say that Pellia, in spite of the small size of its nuclei, is a favorable object for such study. As has just been mentioned, the nucleolus probably contributes something to the substance of the chromosomes. Although the chromosomes are small, they can be distinguished very early and seem to lose their identity much later than is usually the case. Mitoses in the venter of the archegonium show a longitudinal splitting of the chromosomes before the breaking down of the nuclear membrane, while in the germinating spores the splitting occurs much later.

The number of chromosomes in the gametophyte, as counted in the germinating spores and in the actively dividing region of the thallus, is eight. This number, however, is far from being constant. Both Farmer (10) and Davis (7) report occasional irregularities. In the present study, a few nuclei were found with only seven chromosomes, and nine chromosomes were counted in more than a dozen cases (*fig. 20*). Long spindles upon which the chromosomes are irregularly arranged are not infrequent, and it seems probable that such a mitosis might result in an unequal distribution of the chromosomes, and thus account for variations from the typical number (*fig. 8*).

THE THIRD MITOSIS IN THE GERMINATING SPORE.

While considerable attention was given to the third mitosis, an extended description is hardly necessary. Prominent asters

(*fig. 19*) like those of the two preceding mitoses are often present, but they are frequently absent, and the caps appear with only a few radiations (*fig. 18*) or even none at all. There are no radiations in the metaphase (*fig. 7*). In short, it is possible to select from the third mitosis a series of stages identical with a typical series from the apical region of the thallus. At the fourth and succeeding mitoses the resemblance to the usual vegetative divisions becomes more and more pronounced, while asters and centrospheres become correspondingly rare.

THE CENTROSOME PROBLEM.

The centrosome[3] problem is one of extreme difficulty, and perhaps the difficulty is greater for the botanist than for the zoologist. At least, the difficulties are different in the two cases. That there are in animals well-defined centrosomes which function as organs of nuclear division, all investigators agree, and animals or tissues in which centrosomes do not occur are regarded as exceptions. The existence of the organ is not a serious problem; rather, the more recent investigations have sought to establish the permanent or transitory character of an organ which all admit to be present during mitosis. In plants, on the other hand, even the existence of a centrosome is a problem which must be considered separately for the different groups.

It is of interest to note that centrosomes in plants were first observed in diatoms in 1886 by H. L. Smith (31). When Guignard in 1891 published his classic paper on fertilization, botanists at once accepted the results and confirmatory accounts appeared. Strasburger (33) found centrosomes in Larix, Humphrey (18) in Psilotum, Mottier (22) in Delphinium, Schaffner (26) in Alisma and Sagittaria, Campbell (3) in Equisetum, Lauterborn (21) and Karsten (20) in diatoms, and other investigators reported centrosomes in various forms ranging from the algae up to the flowering plants. In fact, the centrosome seemed to be as universally present in plants as in animals. Belajeff (1) and

[3] In referring to flowering plants no attempt has been made to distinguish between centrosomes and centrospheres. In describing mitosis in liverworts some writers have used these terms indiscriminately.

Farmer (11), however, failed to find centrosomes in Lilium. At the same time Strasburger (35), directing a remarkable group of investigators, attacked the problem in all the principal groups of plants. Those who studied thallophytes found centrosomes, but those who studied pteridophytes and spermatophytes not only found no centrosomes, but, in tracing the origin of the multipolar spindle, they found conditions which seemed to preclude any such bodies. Just as the discovery of centrosomes was followed by confirmatory accounts, the multipolar spindle and the non-existence of centrosomes in the vascular plants received immediate confirmation. Guignard, Schaffner, and others still continued to find centrosomes in flowering plants, although these bodies, as represented in the figures, became noticeably less conspicuous than in earlier accounts. In Guignard's (15) recent studies of fertilization no centrosomes are represented in the figures, and no reference to any such structures is made in the text, even during the stage at which the famous "quadrille of the centers" was formerly (14) described. The fact that the great majority of cytologists, with the most approved technique and provided with apochromatic immersion lenses, fail to find centrosomes in flowering plants, added to the fact that the mode of spindle-formation both in reproductive and in vegetative cells, does not require the participation of a centrosome, makes the evidence overwhelming that the centrosome, as an organ of division, does not exist in this group.

In regard to the pteridophytes, the evidence is similar, but not nearly so extensive. The blepharoplasts of pteridophytes and gymnosperms will be considered later.

In the mosses the centrosome problem has received no serious attention, doubtless on account of the small size of their nuclei. Whether there is even a blepharoplast or not still remains to be determined.

In the liverworts, no centrosome is found at any stage in the life-history. However, in Pellia and Conocephalus, and perhaps in all forms with such extensive intrasporal development of the gametophyte, a centrosphere appears during the early divisions in the germinating spore, but even in these few divisions the

centrosphere is very transitory, not persisting from one nuclear division to the next, and appearing only irregularly during the division with which it is concerned. Still, this transitory centrosphere is a functional part of the mitotic figure during the first two or three divisions. In Pellia, at the fourth division, the centrosphere may or may not appear, and in subsequent divisions it was only rarely that we could identify the body at all.

Among the thallophytes, sharply defined centrosomes have been described by competent observers who are thoroughly familiar with all phases of the centrosome problem.

In the fungi, judging from Harper's (16) work on various ascomycetes, a centrosome is present during the period of free nuclear division in the ascus, when it functions in the formation of the spindle. After the period of free nuclear division, the centrosome behaves in a very peculiar manner in forming the young wall of the ascospore.

The centrosome has received more attention in the algae than in the fungi. In papers by Farmer and Williams (12), and by Strasburger (34), centrosomes are described in the oogonia and segmenting eggs of Fucus.

During the early segmentations of the fertilized egg, Strasburger (34) was able to observe the division of the centrosome and to trace its continuity from one cell to another. In the development of the oogonium, however, no such continuity could be recognized. In the large apical cell of Stypocaulon, Swingle (37) found that the centrosome divides, giving rise to the two centrosomes from which the spindle is developed. He was able to recognize the centrosome even during the resting-stage of the nucleus. In the tetraspore mother-cell of Dictyota, Mottier (23) found comparatively large and somewhat elongated centrosomes. These bodies divide and, at least during divisions in the tetraspore mother-cell and in the early divisions of the germinating tetraspore, persist from one cell-generation to another. They develop asters and play an important part in the formation of the spindle.

Lauterborn (21) figures conspicuous centrosomes in Surirella and other diatoms. Karsten (20) also describes centrosomes in

diatoms, and his beautiful preparations, which it was our pleasure to examine, show these bodies as sharply defined as in most animal mitoses. Both Lauterborn and Karsten agree that a centrosome, or at least a body derived from it, becomes cylindrical or ring-shaped, and functions as a spindle during mitosis. The centrosomes of diatoms stain intensely and are not surrounded by a centrosphere. Lauterborn found centrosomes even during the resting condition of the nucleus and cell, but Karsten was not able to identify the body positively until the radiations began to appear. Davis (5) describes a centrosphere, but no centrosome, in the tetraspore mother-cell of Corallina. The centrospheres give rise to the spindle, and consequently play an essential part during nuclear and cell division. No centrospheres could be recognized during the resting-stage of the nucleus.

Thus it appears that in many of the algae well-defined centrosomes are present, at least during certain phases of the life-history, and that the centrosomes may divide and persist from one cell-generation to another, while in other algae the centrosome does not show such a degree of permanence. In the algae which we have mentioned the centrosomes are not surrounded by a clear area. In Corallina it is to be noted that there is no centrosome, but only a centrosphere. In none of the algae have centrosomes been traced throughout the life-history of the plant. In some fungi centrosomes are present during the mitoses concerned in the development of spores. Among the liverworts we doubt whether there is, at any period in the life-history, a centrosome like those described for the thallophytes. The centrosphere, appearing and functioning during only a few mitoses, has replaced the functional centrosome.

The polar radiations which are often conspicuous during mitosis in pteridophytes, gymnosperms, and angiosperms are of the same nature as those of thallophytes and bryophytes, but in the higher groups (and, possibly, in most mitoses in the lower groups) a definite centrosome, or even a centrosphere, is lacking. Centrosomes and centrospheres in vascular plants have been described and figured so frequently by such competent observers

that he would be rash, indeed, who would claim that all such accounts have no foundation except in perverted imagination and preconceived theories. That theories suggested by the accounts of zoologists and supported principally by misinterpretations of plant structures have caused exaggeration in the drawings and descriptions of botanists is probably true. While we believe that most of these centrosomes are to be interpreted as chance granules, nucleoli, pieces of chromosomes, etc., still we see no reason why a centrosome or centrosphere might not occur occasionally through atavism. The finely granular areas which have been noted during spermatogenesis in Coniferales, and the similar areas which are often seen in angiosperms, are, in our opinion, vestiges representing historically the centrosphere as it appears during the early mitoses in the germinating spore of Pellia.

The blepharoplasts described for various pteridophytes and gymnosperms are, in our opinion, to be interpreted as centrosomes. It seems to be true that in Ginkgo (17), Cycas (19) and Zamia (39) they appear only in the body cell and in the spermatozoids. In Marsilea, however, Shaw (29) traced them another cell-generation farther back, and in the same genus Belajeff (2) found blepharoplasts even during the earlier stages in the development of spermatogenous tissue. But granting that the blepharoplast appears during only one or two cell-generations, this does not seem to be a valid argument against its centrosome character, for in Pellia the centrosphere is clearly distinguishable during only a few mitoses, and even in the multicellular thallophytes, if the centrosome should prove to be present throughout the life-history, it is at least much more conspicuous at some phases than at others. Plants furnish numerous illustrations of the gradual reduction, and even the disappearance, of organs during phylogeny. Most botanists admit that in the earliest sporophytes all the cells were sporogenous; but, during phylogeny, portions of the sporogenous tissue became sterilized until the sporogenous tissue finally became much limited in extent and now appears only during a few cell-generations. During such reductions, functions of cells or organs may become completely changed, as in the case of the

elaters of liverworts, which are, historically, sporogenous cells and often develop like sporogenous cells, even up to the spore mother-cell stage. In the formation of the ascospore, the function of the centrosome is not the same as during the mitotic divisions in the ascus. Other examples might be cited.

That the function of the blepharoplast is somewhat peculiar must be admitted. Radiations, however, and spindle fibers, which are often the most conspicuous accompaniments of centrosomes and centrospheres, are actively concerned in movement and are not essentially different from the radiations or cilia of blepharoplasts. In form and function centrosomes present so much diversity among themselves that the peculiarities of the blepharoplast need occasion no surprise. One has only to compare the typical spherical centrosome with the rod-like centrosome of Dictyota, the hollow cylindrical spindle of some diatoms, and with the centrosome which forms the *Hautschicht* of the ascospore.

We should conclude, therefore, that centrosomes, centrospheres, and blepharoplasts are historically related, and with their radiations, spindle fibers, and cilia are only different manifestations of kinoplasmic activity, movement in all cases being the principal function.

Pellia, with the prominent aster and centrosphere of its germinating spore becoming less and less distinct in succeeding mitoses until a condition is reached resembling that which prevails in the flowering plants, presents in its own life-history a great reduction of the aster and the disappearance of the centrosphere.

I am deeply indebted to Professor Strasburger for his kindly courtesy and helpful suggestions during my work in his laboratory.

SUMMARY.

1. The principal part of the work deals with the first three divisions in the germinating spore of *Pellia epiphylla*. We have not intended to attack the excellent work of previous investigators, but rather have attempted to extend a little farther a knowledge of the phenomena of mitosis.

2. A centrosphere, but no centrosome, is very prominent during early prophases of the first mitosis in the germinating spore. The centrosphere is not present at all during the subsequent stages of mitosis. An aster is also conspicuous during the early prophases of the first mitosis, but disappears before the metaphase is reached. Radiations reappear during telophases. The aster is believed to be concerned in separating the poles of the spindle; the radiations during the telophase may be concerned in forming the nuclear membrane or a *Hautschicht* about the nuclear membrane. In the second and third mitoses, the centrospheres and asters become more and more indistinct, and in succeeding mitoses the centrosphere becomes indistinguishable, and a few irregular rays replace the aster.

3. The rays are believed to be lines of streaming material, consisting of the same substance as the centrospheres.

4. Centrosomes, centrospheres, and blepharoplasts are believed to be the same structures historically, being only different manifestations of a common kinoplasmic activity.

5. No centrosomes or centrospheres were found during mitoses in the apical region of the thallus or in developing antheridia. It was not determined whether a blepharoplast occurs toward the close of spermatogenesis.

6. The caps are derived from a *Hautschicht* surrounding the nuclear membrane. The central portion of the spindle is believed to be derived in large measure from the nucleolus.

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EXPLANATION OF PLATES XII–XIV.

All figures were made with a Bausch & Lomb camera lucida, Zeiss apochromatic immersion objective 2^{mm} 1.30 N. A., and Zeiss compensating ocular 12; magnification, about 1,500 diameters. All figures are from *Pellia epiphylla* Raddi, except *figs. 1, 2, 11*, and *12*, which are from *Pellia calycina* Nees.

PLATE XII.

(*Figs. 1–8*, mitoses in germinating spore; *1–6* first mitosis, *7* and *8* third mitosis; *figs. 8* and *10*, mitosis in apical region of thallus.)

FIG. 1. Area about the elongating nucleus has become rather free from starch grains and larger granules. Asters and caps are present.

FIG. 2. Peculiar aster at upper pole; the papilla indicates that it is pulling upon the nuclear membrane.

FIG. 3. The cap is very conspicuous and the nuclear membrane is still intact.

FIG. 4. A cap just beginning to break up into fibers. A transverse section at this stage shows a ring.

FIG. 5. Transverse section of fully formed spindle.

FIG. 6. Mitosis in late prophase; the spindle is evidently made up of two half spindles: radiations conspicuous; definitely formed centrospheres are lacking.

FIG. 7. Metaphase of third mitosis; no radiations or centrospheres are present. Figures of first mitosis are the same at this stage.

FIG. 8. Irregular mitosis (third mitosis) in an unusually large spore, suggesting how nuclei with an irregular number of chromosomes might be formed.

FIG. 9. Mitosis near apical cell; caps prominent and radiations reaching to the *Hautschicht*; at the upper pole is a granule resembling a centrosome.

FIG. 10. Anaphase in mitosis near the apical cell; no asters or centrospheres are present.

PLATE XIII.

(*Figs. 11–17*, second mitosis; *18–20*, third mitosis in germinating spore.)

FIG. 11. Very early prophase.

FIG. 12. Centrosphere and radiations.

FIG. 13. Very prominent centrosphere and radiations. The centripetal ends of the radiations have a pseudopodium-like aspect and suggest that the radiations are lines of streaming material.

FIG. 14. Centrosphere in which the cut end of a fiber resembles a centrosome. There is no centrosphere or aster at the other pole.

FIG. 15. Irregular, elongated centrosphere with prominent aster; no centrosphere or aster at the other pole.

FIG. 16. Tripolar spindle, the third pole not shown. The cut end of a fiber resembles a centrosome. The pull upon the nucleus is evident; upper aster at some distance from the nucleus.

FIG. 17. The two centrospheres are practically alike, but the upper one is shown in median section, while the lower one appears in surface view, the fibers having the appearance of granules within a centrosphere.

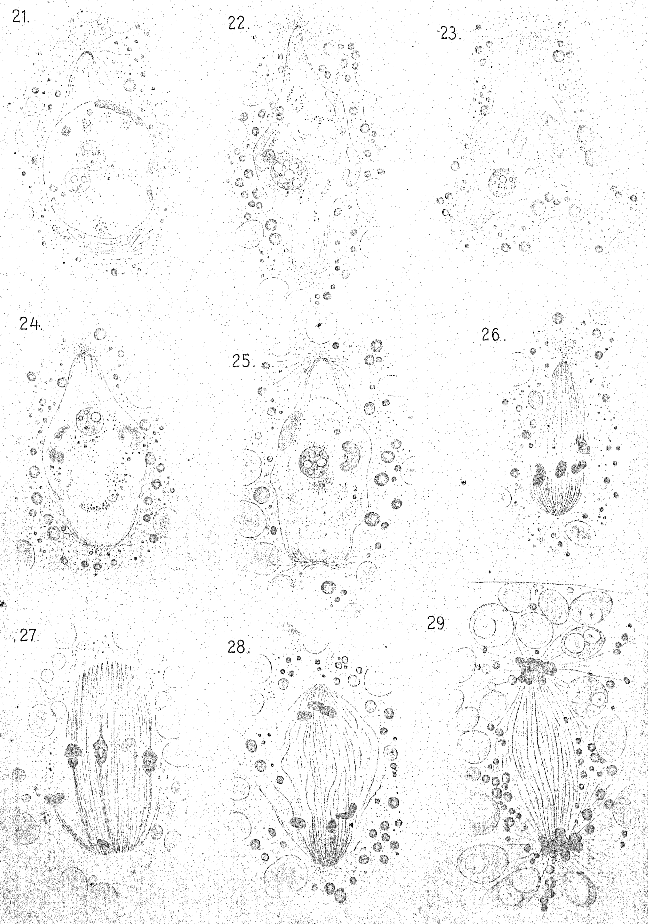
FIG. 18. The more usual appearance of an early prophase at the third mitosis; prominent caps, but no centrosphere or very definite aster.

FIG. 19. An exceptionally prominent centrosphere and aster at the third mitosis; no centrosphere or aster at the other pole.

FIG. 20. Transverse section of mitotic figure at the third mitosis; just before the splitting of the chromosomes, showing nine chromosomes.

Chas. Chamberlain del. Lith.Anst.v.E.A.Funke, Leipzig.

CHAMBERLAIN on PELLIA



Chas. Chamberlain del. Lith. Anst. v. E. A. Funke, Leipzig.

CHAMBERLAIN on PELLIA

PLATE XIV.

(*Figs. 21–29*, second mitosis in the germinating spore.)

FIG. 21. Cap more prominent at upper pole; nuclear membrane intact.

FIG. 22. Nuclear membrane has broken down at the poles, but is still intact at the sides of the nucleus.

FIG. 23. Tripolar figure.

FIGS. 24, 25. Lower cap much broader than the upper; the granular matter within the nucleus is derived largely from the nucleolus and stains with gentian violet.

FIG. 26. Late prophase; the achromatic figure evidently consists of two half-spindles.

FIG. 27. Spindle very broad at the poles; a rather common form at this stage in the first three mitoses; no radiations or centrospheres.

FIG. 28. The caps have kept the ends of the spindle rounded for an unusually long period; no centrospheres or radiations.

FIG. 29. Telophase; radiations, but no centrospheres have reappeared.

NEW WESTERN PLANTS. I.

A. D. E. ELMER.

AGROPYRON SPICATUM **pubescens,** n. var.—A tufted subalpine perennial. Culms slender, 4^{dm} high, cinereous pubescent below the joints. Blades mostly involute, soft pubescent on both sides, pointed, averaging 1^{dm} in length, divaricately disposed; sheaths pubescent, shorter than the internodes; ligule very short. Spike $7–10^{cm}$ long, glabrous or sometimes glaucous; spikelet flattened, 5–7-flowered; glumes abruptly terminated by setaceous points, lower 8^{mm} long, 3-nerved, upper 9^{mm} long, usually 5-nerved; lower palet 5-nerved toward the apex, bearing a slender divergent awn; upper palet equal in length, slightly scabrous on the nerves above the middle, emarginate; stamens 3, anthers 3^{mm} long.

This variety (number 1158) was collected by the writer at an altitude of 1000^{m} on Mt. Stuart, Kittitas county, Washington, in July, 1898. Type specimen is in the herbarium of Stanford University.

Festuca arida, n. sp.—A loosely tufted fibrous rooted annual, turning purplish at maturity. Culms varying from $3–13^{cm}$ in length, geniculate at the lower joints, striate, nearly glabrous. Leaves $1–5^{cm}$ long, involute, smooth outside, canescent inside; sheaths exceeding lower internodes, margins overlapping, smooth, the upper one inflated and partially inclosing the young inflorescence; ligule very minute, brownish. Panicle at maturity exserted, divaricately branched; rays usually single, ridged, puberulent; spikelets few, secund, sessile, 6^{mm} long, 2–3-flowered from near the base; glumes entirely smooth, unequal by 1^{mm}, lower sharply acuminate and 1-nerved, upper 3-nerved, 6^{mm} long; lower palet 5-nerved, nearly 6^{mm} long, ciliate with long and dense hairs over the entire back, bearing an awn 5^{mm} long; upper palet of equal length, rather broad from the middle toward the base, acuminate toward the apex, hyaline except the two nerves which terminate in fine bristle-like points; anthers

very short; seeds 4^{mm} long, brown, lanceolate, grooved on one side.

In habit this plant resembles *F. microstachya* Nutt. from which it is separated by its dense evenly ciliate lower palet, and from *F. microstachya ciliata* Gray by its glabrous glumes. This species (number 2196) was collected by Professor *L. F. Henderson* at North Yakima, Yakima county, Washington, May, 1892. Type specimen is in my herbarium.

Festuca idahoensis, n. sp.—Apparently a perennial, from creeping rootstocks. Culms striate, shining, $7-9^{dm}$ high, 2–3-jointed. Cauline leaves few, filiform, those of the sterile shoots equaling or exceeding the culms, striate, glabrous beneath, involute, less than 0.5^{mm} in diameter, canescent inside; sheaths loose, striate, smooth, the throat abruptly constricted at the leaf base; ligule a brown narrow fimbriate band. Panicle ovate, $7-12^{cm}$ long; rays 2, spikelet-bearing from below the middle; spikelets few, loosely 3–4-flowered, 10^{mm} or less long; glumes glabrous, broad, 3-nerved, upper 4^{mm} long and obtuse, lower acute, 3^{mm} long; lower palet broadly lanceolate, obscurely 5-nerved, 6^{mm} long, bearing a scabrous awn 3^{mm} long; upper palet equal in length, quite broad, 2-nerved, slightly bidentate at the apex; each of the 3 anthers 3^{mm} long; styles 2, distinct, upon the obovoid ovary.

This fescue grass is distinguished from *F. rubra* L., which it resembles, by its extremely long filiform leaves. It was collected by Mr. *L. R. Abrams*, in Smith's Valley, Shoshone county, Idaho, July, 1900. Type specimen (number 688) is in Mr. Abrams' herbarium.

Bromus magnificus, n. sp.—A scattering perennial, with creeping rootstocks, bearing few slender woolly fibrous roots. Culms $1-3^{m}$ tall, shining, erect, with 6–9 densely pubescent joints. Blades flat, scabrous on the edges, 7^{mm} wide, the larger ones 3^{dm} long, upper surface puberulent with few bristle-like hairs, lower surface glabrous, apex acuminate; sheaths soft, equaling the internodes, conspicuously striate, entirely covered with long soft retrorse hairs; ligule brownish, 2^{mm} long. Panicle not drooping, pyramidal in outline, 25^{cm} long, nearly the same in diameter at the base; rays 2–3, long and slender, subtended by a circle of fine hairs, pendulously flexuose, 1–2-branched from the middle, scabrous near the distal ends; spikelets soft,

2–3 ^{cm} long, flattened, attenuate toward the base, 7–9-flowered; glumes unequal by 1 ^{mm}, upper one 8 ^{mm} long and 3-nerved, lower 1-nerved, pubescent, both acuminate with a point 1 ^{mm} long; rachilla pubescent; lower palet pubescent around the base and on the sides below the middle, the upper half becoming scabrous, 12 ^{mm} long, prominently 3-nerved and often with minor ones between, bearing a straight scabrous awn 5 ^{mm} long; upper palet shorter by 3 ^{mm}, long-ciliate on its 2 nerves; stamens 3, their anthers nearly 3 ^{mm} long; styles 2, from below the bristle covered callous cap.

This magnificent Bromus was found by the writer only in a small shaded boggy district near Port Angeles, Clallam county, Washington, August, 1900. I have the identical species duplicated in a specimen from Yes Bay, Alaska, collected by Mr. *T. Howell*, in 1885, number 1722A. Professor C. L. Shear in his revision of the genus refers Howell's specimen to *B. sitchensis* Bong., from which it is at once separated by its pilose nodes, sheaths, and spikelets. It is most nearly related to *B. pacificus* Shear, from which it differs in its much larger size, the smooth lower surface of its leaves, the lax panicle whose rays are not secund, the slender-pointed glumes, and much shorter upper palet. Type specimen (number 1957) is in the herbarium of Stanford University.

Panicularia multifolia, n. sp.—A weak subaquatic perennial, with slender creeping rootstocks bearing fibrous roots at the nodes. Culms generally reclining, 9–12-jointed, rather soft in texture, 7–9 ^{dm} long. Blades all cauline, as many as there are joints, flat, glabrous on both sides, finely scabrous along the margins, the largest ones 14 ^{cm} long and 10 ^{mm} wide, gradually diminishing in size, all acuminately lanceolate; sheaths glabrous, the upper ones exceeding the internodes; ligule 3 ^{mm} long, hyaline, becoming lacerate. Panicle ovate, 5–8 ^{cm} long by 3 ^{cm} wide at the base, strict; rays 2, rigidly flexuose, smooth or slightly scabrous, with 3–5 spikelets, branched from below the middle; spikelets not compressed, 3–5-flowered, falling extremely early, the largest ones 5 ^{mm} long; marginal apex of the persisting glumes hyaline, subequal, lower 1 ^{mm} long, upper broadly spoon-shaped; lower palet conspicuously 5-nerved, obscurely scabrous on the margin and the nerves, 3 ^{mm} long, broadly elliptical, the hyaline apex subtended by a narrow brown band; upper palet a trifle

shorter, scabrous on the two nerves, notched at the apex, sides hyaline; anthers a little longer than 0.5^{mm}; styles 2, separate, inserted on the glabrous ovary.

This Panicularia was discovered in a subalpine open boggy place in the woods of the Olympic mountains (elevation $1,000^{m}$), Clallam county, Washington, August, 1900. It is at once distinguished from *P. pauciflora* (Presl.) Kuntz, by its slender many jointed leafy stem, the uniformly small rigid panicle, and the very early falling of the flowers, leaving the glumes still attached. Of this rare species the type specimen (number 1939) is in the herbarium of Stanford University.

Panicularia flaccida, n. sp.—A tall perennial, from slender creeping rootstocks. Culm $1–2^{m}$ high, smooth and shining, 5–7-jointed, rather soft and reclining. Blades as many as there are joints, flat, finely scabrous on both sides, flaccid, $12–15^{mm}$ wide, averaging 2^{cm} long, lanceolate acuminate, with a strong midnerve from the base; sheaths a trifle shorter than the internodes, glabrous, many striate; ligule membranous, hyaline, $2–3^{mm}$ long, ultimately becoming lacerate. Panicle lax, subpendulous, $15–20^{cm}$ long, $9–15^{cm}$ in diameter; rays 2, 3, or 5, usually branched from or below the middle, slender, lax and flexuose, slightly scabrous on the ultimate branches; spikelet $3–5^{mm}$ long, compressed, 5–7-flowered, soft in texture; glumes persistent after the breaking up of the flowers, the upper half hyaline or in age entirely so, nerveless, glabrous, the lower 1^{mm} long and obtusish, the upper a trifle longer and ladle-shaped; rachilla 5^{mm} long, terminating in a rudimentary flower; lower palet broadly elliptical, finely scabrous on the conspicuous 5 nerves, 2.5^{mm} long, the upper margin hyaline; upper palet 2^{mm} long, rather broad, obscurely scabrous on the 2 nerves above the middle, apex with a shallow notch; stamens 3, with anthers 0.5^{mm} or a trifle longer; styles 2, distinct.

This grass is separated from *P. pauciflora* (Presl) Ktz. by its taller, more flaccid habit, pale color, and the larger lax panicle. It was collected by myself in a shaded boggy place in the foothills of the Olympic mountains, Clallam county, Washington, July, 1900. Type specimen (number 1940) is in the herbarium of Stanford University.

Poa laeviculmis Williams,[1] n. sp.—A robust, densely tufted,

[1] In a recent communication from Professor W. J. Spillman, Agrostologist of the Bureau of Plant Industry, U. S. Department of Agriculture, concerning this grass, I

glabrous, glaucous perennial, 7–10^{dm} high, with linear, plane, or mostly involute leaves, and exserted rather densely flowered panicles 1.5–2^{dm} long. Culms glabrous throughout; sheaths glabrous, shorter than the internodes; ligule firm, truncate, 1–2^{mm} long; leaf blades rather firm, usually involute, at least when dry, scabrous only on the margins, those of the culm 1–2^{dm} long, 3–4^{mm} wide, those of the innovations often 3^{dm} in length. Panicle lanceolate, 1.5–3^{cm} in diameter, pale or purplish, rachis nearly glabrous, branches erect or ascending, fasciculate, rather densely flowered, scabrous, the lower ones 5–7^{cm} long. Spikelets lanceolate, 6–10^{mm} long, 4–6-flowered; empty glumes lanceolate, acuminate, 3-nerved, scabrous on the keels, the first 3.5–4^{mm} long, the second somewhat longer; flowering glumes lanceolate, acute, about 5^{mm} long, faintly 5-nerved, minutely punctate scabrous throughout, basal hairs entirely wanting. Palea about equaling the glumes, ciliate scabrous on the keels.

Type specimen collected at Steptoe, Washington, *G. R. Vasey*, number 3026, June 25, 1900. Numbers 3034 and 3028, *G. R. Vasey*, June 1, from the same locality, are referred here, as well as number 2421A, *W. C. Cusick*, Wallowa county, Oregon, June, 1900. Number 3028 *Vasey* cited above is a very glaucous form with plane leaves, but otherwise like the type. It is closely related to *Poa nevadensis*, but is distinguished by its more robust habit, and glabrous leaves and culms. In *Poa nevadensis* the culms are decidedly scabrous below the panicles and the leaves are very scabrous. From *Poa ampla* this species is distinguished by its more strict panicles, more numerously flowered spikelets, and absence of a rootstock.

Puccinellia rubida, n. sp.—A densely tufted biennial, from numerous fibrous roots. Culms few, erect or geniculate below, slender, 2–3^{dm} long, smooth, naked from the middle, usually of a dark red color. Leaves very numerous from the base, 3–7^{dm} long, mostly falcate, strongly involute, smooth and glaucous on the outside, scabrous along the edges, rigid and pungently pointed, cauline ones 2 or 3, very short; sheaths longer than the internodes, smooth, glaucous green to purplish; ligule 1^{mm} long,

received a copy of Mr. T. A. Williams' diagnosis of this species. Professor Spillman kindly suggested that I include it for publication in this article, with an explanation that it has been in manuscript for some two years and would have been published sooner had it not been for Mr. Williams' death.

entire, obtuse, decurrent on the margins of the sheaths. Purplish panicle ovate, $3–7^{cm}$ long; rays 2–4, unequal in length, ascending, scabrous toward their distal ends, branched beyond the middle; spikelets usually 3–5-flowered, 5^{mm} long, narrowly lanceolate to linear, upon thickened purplish pedicels; glumes obscurely nerved, glabrous, purplish, lower broadly obovate and a trifle longer than 1^{mm}, upper 2.5^{mm} long, 3-nerved at the base; lower palet obscurely 3–5-nerved, of the same purple color except the brown hyaline tip, obtuse, averaging 3^{mm} long, broadly elliptical; upper palet at least equal in length, bifid, slightly scabrous on the 2 nerves above the middle; stamens 3, the anthers linear and nearly 2^{mm} long; rachis thickened at the insertion of the flowers, puberulent, terminating in a rudimentary flower, each of the joints about 1.5^{mm} long; styles 2, with rather short and sparsely plumose stigmas, inserted separately upon the glabrous ovary; lodicules present.

This grass is certainly closely allied to the genus Poa, in distinction from which it is chiefly characterized by its linear spikelets, shorter and very unequal glumes; it also bears a strong resemblance to the genus Panicularia, from which it is at once distinguished by its obscurely nerved glumes and palets. It is unlike *P. lemmoni* (V.) Scb. in its smaller size, purplish culms and panicles, appressed and fewer flowered spikelets. Mr. *Wm. C. Cusick* collected it in a moist alkaline meadow at Cold Spring on the Burns-Prineville road of Crook county, Oregon, June, 1901. Type specimen (number 2621) is in my herbarium.

Sitanion albescens, n. sp.—A cespitose annual or biennial, with smooth or sparsely woolly cord-like roots. Culms many, $1–2^{dm}$ high, erect, striate and glaucous green below the spike, barely exceeding the uppermost sheath. Blades numerous, coriaceous, crowded below the middle of the stem, rigidly involute, smooth and light green on the outer surface, ridged and cinereous pubescent on the inner side, slightly scabrous along the edges, usually slender and ascending, $3–8^{cm}$ long; sheaths overlapping, striate, smooth, glaucous green, persistent and marcescent near the base, open at the throat; ligule 5^{mm} broad, frequently produced on the sides into callous tips. Spike 7^{cm} long, barely exceeding the leaves, breaking up readily at its nodes, light green when in flower but soon turning purplish-gray; internodes of

rachis $3-4^{mm}$ in length, much flattened, with or without a cinereous pubescence on its edges; spikelets usually 2 at each joint, though frequently one of them is entirely sterile, $3-4^{cm}$ long including the awns, 1-3-flowered; glumes 5-7, generally entire, 7^{cm} long, 1-3 striate, smooth or finely pubescent, gradually tapering into a slender scabrous awn 3^{cm} long which is strongly recurved in age; lower palet nerveless except toward the apex, $7-10^{mm}$ long, coriaceous, smooth or puberulent, finely scabrous on the nerves above the middle, extending into an awn $2-3^{cm}$ long; upper palet 8^{mm} long, the two nerves smooth or slightly scabrous toward the bidentate apex; stamens 3, anthers 2^{mm} long; styles 2, from the apex of the ciliate callous cap of ovary; caryopsis short, stipitate at the base, smooth, plump, with a groove on the side of the upper palet.

This species was collected in the valley north of Ellensburg, Kittitas county, Washington, by *Kirk Whited*, June, 1898. It is distinguished from *S. glabrum* Sm. by its more cespitose habit, and usually by its slender rigidly involute leaves, whose sheaths are overlapping. Type specimen (number 670) is in Mr. Whited's herbarium.

Sitanion ciliatum, n. sp.—A tufted annual or biennial from strong rigid roots usually covered with a woolly matrix. Culm $1-2^{cm}$ high, striate and cinereous pubescent just below the inflorescence, strictly erect, clothed at the base with marcescent sheaths. Leaves numerous from sterile shoots, convolute to involute, averaging 7^{cm} in length, pungently pointed, upper surface glaucous and finely scabrous on the striae, lower surface covered with a close cinereous and usually with a longer ciliate pubescence; cauline leaves flat and broader; sheaths at least equaling the internodes, open at the throat, the lower ones cinereous and ciliate pubescent, the uppermost one cinereous pubescent and loosely including the culms; ligules very narrow, on the sides often developed into callous protuberances, decurrent down the sheath margin as a hyaline membrane. Spike 7^{cm} long, densely virgate, purplish brown at maturity, readily breaking up at the joints; 2 spikelets at each joint, one of which is frequently sterile, $3-4^{cm}$ long including the awns, 1-3-flowered; rachis joints $3-4^{cm}$ long, compressed, smooth or with sparse cilia along

the edges; glumes 4–6, bifid to the base, narrow, 1–3 striate, nearly smooth toward the base, scabrous on the nerves, about 10^{mm} long, gradually tapering into a scabrous awn $3–4^{cm}$ long which is strongly recurved in age; lower palet 8^{mm} long, puberulent or scabrous on the 5 nerves, extending into a scabrous purplish awn $3–4^{cm}$ long; upper palet equal in length, finely scabrous on the 2 nerves above the middle, bidentate; anthers of the stamens 2^{mm} long; styles 2, from the ciliate callous cap of the ovary; the two lodicules conspicuous; seed 6^{mm} long, pointed at the base, grooved on the side of the upper palet.

It is quite similar to *S. albescens* Elm., but may be recognized by the cinereous and ciliate pubescence of the sheaths and leaves. They may be found to intergrade, yet it seems best to recognize them as two forms. Mr. *Kirk Whited* collected it on dry rocky hills west of Wenatchee, Chelan county, Washington, June, 1901. Type specimen is in my herbarium.

Sitanion strictum, n. sp.—A densely tufted annual or biennial, with cord-like roots covered with a woolly matrix. Culms strict, $2–4^{dm}$ high, pubescent or nearly glabrous below the inflorescence. Leaves erect, conduplicate to involute, slender, sharply pointed, striate, villous on both sides, lower surface greenish, upper paler; sheaths equaling the internodes, striate, soft pubescent, usually overlapping, the upper ones loosely inclosing the stems, the basal ones persistent and becoming marcescent; ligule nearly obsolete. Spike light green, subflexuose, generally much exceeding the upper sheath, $7–11^{cm}$ long; spikelets 2 at each joint, 1–3-flowered, the lower flower usually fertile, $4–6^{cm}$ long including the awns, readily breaking up at the joints; rachis 4^{mm} long, compressed, shining straw color; glumes 6–8, entire or parted from near the base and of different lengths, scabrous along the hyaline margins and on the strong ridge-like nerves, gradually extending into a slender scabrous awn 4^{cm} long; lower palet puberulent for the lower two-thirds, scabrously 5-nerved toward the apex, 10^{mm} in length, generally bearing 2 short bristle-like awns at the point of insertion of the slender scabrous awn $3–5^{cm}$ long; upper palet equal in length, scabrous on the 2 nerves toward the apex, terminating in 2 unequal bristle-like scabrous awns; stamens 3, anthers 2^{mm} long; the 2 styles distinct; ovary

with a ciliate callous cap; caryopsis 6^{mm} in length, plump, pointed at the base, longitudinally grooved on the side toward the upper palet.

This species has been confounded with *S. villosum* Sm., from which it is separated chiefly by the character of the leaves. In typical *S. villosum* Sm. the basal leaves are short, flat, and rigid; the cauline ones are also rigid, flat, tapering from the base to the pungently pointed apex, and they are usually divaricately disposed. This species is far more common throughout the plains of eastern Washington, while *S. villosum* Sm. was discovered on rocky exposed points along the Snake river. Type specimen was collected by the writer at Parker Station, Yakima county, Washington, July, 1898, and is in my herbarium.

Hypericum bryophytum, n. sp.—A loosely tufted subaquatic annual, with smooth fibrous roots. Stems densely covered with foliage, glabrous, $2–5^{cm}$ long, rather weak, procumbent and branched near the base. Leaves opposite, obtuse, ovate to oblong or obovate, entire, larger ones 5^{mm} long and almost as wide, sessile, ascending, attached by a broad base, usually much overlapping, glabrous or glaucous on both sides. Flowers solitary or rarely cymosely disposed, small, barely surpassing the upper pair of leaves; the 4 sepals persistent, distinct, ascending, glabrous, usually obovate, 3^{mm} long; petals 4, very thin, shorter than or equaling the calyx, deciduous or soon withering, deep yellow, elliptical or obovate, delicately nerved, with a fine fringe of hairs along the upper edge, otherwise smooth; stamens numerous, equaling the corolla, separate, anthers orbicular; styles 3, distinct, persistent, slightly exceeding the stamens, terminated by small capitate stigmas; capsule septicidally dehiscent, tricarpellary, many seeded; seeds light brown, cylindrical, 0.5^{mm} long, puberulent, longitudinally striate.

This is a strictly alpine species, which in its native place is invariably associated with mosses, to which it bears a strong resemblance. It has frequently been referred to *H. anagalloides* C. & S., which has usually a lower altitudinal range and from which it differs in its smaller size, more numerous leaves, and fewer flowers. I collected it above timber line in the Olympic mountains, Clallam county, Washington, August, 1900. Type specimen (number 2833) is in the herbarium of Stanford University.

Orthocarpus olympicus, n. sp.—An erect annual, $2–3^{dm}$ high. Stems smooth, slightly angular, usually dark brown on the

angles, fastigiately 1–5-branched from above the middle, branches sparsely pubescent. Lower leaves entire, ascending, lanceolate, deciduous, the larger ones 4^{dm} long, plainly 3-nerved from near the base, puberulent on both sides, the uppermost with 2 narrow lateral lobes. Spike erect, 2^{cm} in diameter, cylindrical, not rigid, usually compact; bracts short petioled, membranous, finely hispid on the edges, elsewhere puberulent, apex of the upper ones rose-purple and nearly truncate, attenuate at base, with reticulate veins between the 3 nerves, scarcely exceeding 1^{cm} long and only 1^{cm} wide including the sharply acuminate lateral lobes $3–5^{mm}$ long; flower short peduncled, in the axil of the bract; calyx 7^{mm} long, somewhat saccate, hyaline except the 4 long ciliate nerves which terminate in delicate scabrous points 1^{mm} long; corolla tubular, bilabiate, 12^{mm} long, constricted just below the middle and bent upward, only the tips dull purple, conspicuously 12-nerved around the base; lower lip broadly obtuse, with 3 obsolete barely apiculate lobes, faintly canescent; upper lip slightly exceeding the lower, triangular, obscurely canescent, with a short blunt recurved apex; stamens 4, inserted on the corolla tube, mostly inclosed by the upper lip; anthers 2, oblong, 2-celled, the lower cell nearly equaling the upper; style equaling the stamens, the small stigma terminal; capsule puberulent, obovoid, loculicidally dehiscent; seeds not numerous, arranged on a central placenta, falcate, plump, 1.5^{mm} long, with narrow irregular corrugated wings.

This species was collected by the author in the Olympic mountains, Clallam county, Washington, August, 1900, at an elevation of 1000 to 1500^{m}. It seems to be rare, and in my opinion it is wholly unlike *O. imbricatus* Torr. in its smaller, less coriaceous, and broadly obtuse or truncate bracts. Type specimen (number 2574) is in the herbarium of Stanford University.

HERBARIUM OF LELAND STANFORD JUNIOR UNIVERSITY.

BRIEFER ARTICLES.

POSITIVE GEOTROPISM IN THE PETIOLE OF THE COTYLEDON.

(WITH ONE FIGURE)

In a former paper[1] on the geotropic responses of young hypocotyls and the cotyledons of some monocotyledons, I showed that the downward curves they execute are in response to stimuli received by the root tip. This note is to report the same phenomenon in yet another category of stem-organs—in the petiole of the cotyledon. The accompanying figure shows a seedling of *Aesculus Californica*. When the buckeye germinates, the first structures to elongate are these petioles, and in whatever position the seed is lying they grow enough to bend in such a way that when the active growth of the root begins it is directly downward. I have observed the germination of the seeds in all cardinal positions and found this true, whether the curve was alike in the two petioles or was accomplished by more rapid growth of either one.

The analogy to the positive geotropism in cotyledons and hypocotyls is close enough to convince one that these petioles act under the influence of the root tip. Measurements of the growing region corroborate this view. In a rather advanced seedling, whose root was already 7^{mm} long at the beginning of the experiment, the growing region was more than 15^{mm} long. It was placed horizontal and left 29 hours, and by that time the tip was aimed almost vertically downward. The most considerable elongation was in zones 6–8, but it amounted to 3^{mm} (measured midway between the convex and concave sides) between the 10^{mm} and 15^{mm} lines. The curve began about the 14^{mm} mark, and had the least radius at about 12^{mm}, but continued toward the tip into zone 6.

In this case there was evidently an apical growing region, consisting partly of root and partly of shoot, which curved where it grew. Likewise in both root and shoot the curvature was at first more largely

[1] Bot. Gaz. 31:410. 1901.

in the shoot, while before the close of the 29 hours the zone of most rapid elongation had moved forward into the root. So far as concerned its geotropism it behaved as if all root. In older roots the growing region is shorter, as would be expected in correlation with their being decidedly more slender, and the curve is correspondingly nearer the tip. As the cotyledons serve solely as a food store, they remain in or on the ground, where the seed germinates, and there is no later growth with negative geotropism, such as occurs, for instance, in the hypocotyl of Lupinus.

A hypocotyl is practically absent in the Aesculus seedling, the root beginning hardly a millimeter below the insertion of the petioles of the cotyledons. The lower part of these petioles, however, grows more or less firmly into a tube by the coalescence of their margins. The curve may occur in this tube, as in the figured and measured specimens, or in the upper ends where they are usually separate. The tube entirely surrounds the plumule, and the curve is ordinarily far enough up in the petioles so that the lower end of them with the enclosed plumule is brought into the vertical line with the root.

The plumule being below the curve, and already in the vertical line, when it grows it does not escape from the petiole-tube by growing out of the top of it, but out through its side. It does not have to force this passage, which it could hardly do. But at the height where it is to escape, and on that side, there is a vigorous but strictly localized growth, without a corresponding elongation elsewhere in the same zone. The result is the same as when the two guard cells of a stoma with rigid, fast ends enlarge; they spread apart in the middle. In the same way the two petioles pull, or rather push, apart, opening a wide crack, often two or three times as wide as it need be, to permit the free growth of the plumule. What stimulus determines this remarkable localized growth I do not know.

This buckeye is very abundant here, and its large seeds with powerful roots make it an inviting subject for any work on the pressure exerted by the growing roots, or involving their mutilation. For these ordinary experiments on geotropism, reported here, it is well adapted, because it can easily be marked accurately, and especially because of the ease of fixing the position. The cotyledons are so large and heavy that it is only necessary to make plane the proper side and put the seedling down on that surface in a dish containing a little water. The plane of the cut surface determines the inclination of the growing region. If older seedlings are to grow downward, the cotyledons

are cut in the same way and then placed on pedestals. When the whole active part of the seedling is under water growth ceases, but in moist air they do very well. Seeds kept some months in the very dry air of the laboratory refuse to germinate.—EDWIN BINGHAM COPELAND, *Stanford University, California.*

CONTRIBUTIONS TO THE BIOLOGY OF RHIZOBIA.

III. NOTES ON THE WINTER AND EARLY SPRING CONDITIONS OF RHIZOBIA AND ROOT TUBERCLES.

THE major observations here recorded were made during the winter and early spring of 1893 and 1894; incidental observations were also made during subsequent winter seasons. The object was to obtain more definite information regarding the permanency of leguminous root tubercles and the viability and natural resistance of rhizobia to low temperatures, more especially low temperatures with frequent changes to higher temperatures as in the winter months of the central states, Illinois in particular. Sudden changes of temperature, though not necessarily fatal to life, have a pernicious effect upon low organisms. The effects of temperature and other climatic conditions become gradually less with increase in depth of soil. The organisms found in the surface soil are most directly exposed to the pernicious climatic changes.

From the following table of mean monthly averages for the months of November, December, January, February, and March, 1902–3, with a list of coldest days of each month, it will be seen that the variation in temperature was considerable. Very cold weather (– 10° to – 15° F.) did not continue for more than a few days at a time.

Month	Min. ° F.	Max. ° F.	Mean ° F.	Coldest days ° F.
November	25.9	52.1	37.3	6, 10, 14, 16, 18, 18.
December	19.9	38.4	30.0	– 6, 1, 3, 5, 6, 6, 8, 9.
January	20.3	39.7	29.4	–21, –12, 12, 10, 12.
February	15.6	33.9	24.7	– 5, 2, 3, 3, 7, 8.
March	32.9	55.6	43.5	10, 11, 12, 16, 21.

The humidity during the months indicated was somewhat above the average for the state of Illinois. The ground was covered with snow during parts of the months of January, February and March. Soil covered by snow banks was not frozen at any time. The open unprotected soil was frozen to a depth of about eighteen inches during January, February and the early part of March.

The prevailing opinions held have been that leguminous root tubercles are destroyed at the close of the seasonal vegetative period and that the cytoplasmic and albuminoid contents of rhizobia are absorbed or assimilated by the host plant. Upon examining the roots of *Trifolium pratense* late in November it was found that the tubercles present were normal in appearance. Microscopic examination showed that rhizobia (*R. mutabile*) were present in smaller numbers than during the summer months. The highly refractive sporoids (fatty particles) were more plentifully present and more distinct. Since the tubercles were intact the question arises, what became of the missing rhizobia? It is highly probable that through lack of nutriment they became famished and finally died. Most organisms present reacted very feebly with the usual cytoplasmic stains, indicating a reduction in the cytoplasm. In such rhizobia the above mentioned sporoids were very distinctly visible and took the stain readily. Each organism showed from one to five such sporoids, more usually one in the neck portion and two or sometimes three or four in the body of the Indian club-shaped rhizobia, and quite generally occupying a position next to the cell-wall. They are not uniform in size and form. They stain a reddish brown with iodin tincture and are very clearly shown in an aqueous solution of corrosive sublimate. Infecting threads (Infectionsfäden) are present in apical areas and show no special modifications. In some tubercles they seemed to be wholly wanting. When present they are usually very distinct for several reasons, because of the lesser abundance of rhizobia and also because of the greater thickness of the cellulose wall. They are almost entirely empty, containing only a few small motile forms of the rhizobia. The walls of the filaments attain their maximum thickness late in the fall of the first season; the following season they do not increase in thickness, though they become refilled with motile rhizobia, finally rupturing the wall or escaping through breaks already existing. Thus they again refill the cells with mature, greatly modified, non-motile rhizobia. During the second year's growth of the tubercles, the filaments often disappear entirely. They may be destroyed or assimilated by the rhizobia or by the host plant. In some instances the filaments become separated from the cell-walls because of the tension due to the growing cell. The separation may take place in any part of the threads, but more commonly where they unite with the cell-wall. During the second season the partially emptied infected area of tubercles again becomes tensely filled with mature rhizobia, through the multiplication of organisms

found in the infecting threads which are found in the apical areas of tubercles and in the cells just within the phellogenic layers. Additions to the growth of the tubercles are also made at these points. The starch, which was deposited just outside of these meristematic areas in the fall of the year, is now again assimilated by the host plant.

It is evident that perhaps about one-half, or somewhat less, of the rhizobia existing within the infected areas of tubercles are killed during the unfavorable winter conditions. Freezing alone does not kill them; it is rather a combination of conditions, the lack of food supply perhaps being the most important. The tubercles and soil examined were taken from near the surface of the frozen ground when the temperature was from -10° to -20°F. Cultures were made from the tubercles as well as from the soil by the usual plate isolation methods. The growths showed the presence of rhizobia and other soil bacteria. Streak and stab cultures were also made from the infected area of tubercles. A careful examination of growths and culture media at the point of inoculation showed a number of impoverished tubercle organisms which had evidently lost the power of dividing. These stained very feebly and the cell-wall was partially destroyed, having a roughened perforated appearance. Soil cultures showed the presence of rhizobia, besides numerous soil bacteria.

Examining tubercles which were more deeply situated, about one foot below the surface of the soil, showed that the destruction of rhizobia had been less and the number of dead but not destroyed rhizobia was also less, which would seem to indicate that cold was also a factor to be considered in the killing of rhizobia. It seems probable that rhizobia of tubercles below the freezing depth develop and multiply to some extent, though the tubercles do not increase in size, as is indicated by the tensely filled glistening appearance of such tubercles. A careful examination of a number of such tense, brittle tubercles showed that they contained numerous rhizobia imbedded in a large amount of a mucilaginous substance. The cells of the infected area were loosely united and almost spherical in form. The contents of these tubercles require further study.

The observations were made chiefly upon tubercles of *Melilotus alba*, *Trifolium pratense*, and *T. repens*, and the conclusions with reference to these plants are that root tubercles are mostly biennial, the tubercles attaining their full growth during the first year and gradually dying and decaying toward the close of the second year.[2] With the

[2] New tubercles are, of course, added each season along with the development of new rootlets.

death and decay of the tubercles most of the contained rhizobia also die, but some escape into the soil and serve to infect other roots of the same host species. No comparisons were made between summer and winter soil to determine the comparative number of rhizobia present. It is, however, highly probable that the conditions are much as with the rhizobia of summer and winter tubercles. The tubercles of annuals, like the bean, pea, Spanish pea, etc., die and decay at the close of the vegetative period and many of the contained rhizobia escape into the soil. Many are no doubt killed and assimilated by the host plant shortly before the close of the vegetative period; according to some authorities during the seed- and fruit-forming period of the host plant.

The following are the conclusions based upon the observations recorded:

1. A considerable number of rhizobia of biennial and perennial plants forming root tubercles are killed during the winter months.

2. Root tubercles of perennial herbaceous legumes attain their full growth during the early part of the first season.

3. Most root tubercles of perennial herbaceous legumes die and decay at the close of the second season, returning only a part of the contained rhizobia to the soil. Many of the rhizobia are assimilated by the host plant during the period of fruit development.—ALBERT SCHNEIDER, *California College of Pharmacy, San Francisco.*

CURRENT LITERATURE.

BOOK REVIEWS.

Bacteriology.

THE American edition of Muir and Ritchie's well-known *Manual of Bacteriology*, edited by Dr. N. McL. Harris, is a worthy representative of American bacteriology.[1] The manual, designed primarily for medical students, has been greatly improved by Dr. Harris by additions at points where the previous English editions were lacking. The increase in size to octavo and the introduction of a number of new illustrations, including some photomicrographs of excellent typographical execution, add much to the general appearance of the book, while the enlarging of the chapters on methods brings the manual nearer to the student as a source of practical information on laboratory technique.

The importance of sanitary bacteriology is recognized by the introduction of a new section on "Bacteria in air, soil and water." The increasing scope of bacteriological examinations in preventive medicine would perhaps warrant even more extensive consideration than is accorded to the subject. The chapters on the special diseases have been revised to include our more recent knowledge of bacterial etiology and diagnosis, and the theories regarding immunity are set forth in so lucid a manner that the student should obtain a most excellent working basis for further study.

As in previous editions, the style of the manual is interesting and the reader is more than ever impressed with the author's conception of bacteriology as an organic part of pathology and medicine.—E. E. IRONS.

MINOR NOTICES.

VON WETTSTEIN[2] has recently published a second paper on Neo-Lamarckian principles in relation to Darwinism. His position is a somewhat intermediate one between these extreme schools, whose views are discussed in relation to one another and to the mutation theory of DeVries. —B. M. DAVIS.

Trees and Shrubs, number 2, by Charles S. Sargent,[3] was issued in May, 1903, and contains illustrations of two species of Guatteria from Central

[1] MUIR and RITCHIE, Manual of Bacteriology. 8vo. pp. xx + 565. New York: The Macmillan Company. 1903. $3.50.

[2] WETTSTEIN, R. VON, Der Neo-Lamarckismus und seine Beziehungen zum Darwinismus. pp. 30. Jena: Gustav Fischer. 1903. *M* 1.

[3] SARGENT, C. S., Trees and shrubs, pt. II, pp. 51–99. *pls. 26–50.* Boston and New York: Houghton, Mifflin & Co. 1903. $5.00.

America, descriptions and plates of eight new species of Crataegus, one of Malus, one of Solanum, one of Picea, and a new hybrid Cornus. There are also illustrations and descriptions of thirteen other species, previously described elsewhere.— C. R. B.

THE CHARALES of the province of Brandenburg have been described by Holtz[4] in an account of 136 pages which is well illustrated. This volume is one of a series that is to treat the cryptogamic flora of this region. The account of the general structure of this group is very clear, the notes on distribution are full, and the arrangement good. It seems to be an excellent piece of work of its character.— B. M. DAVIS.

RINGLE AND KENOYER have attempted to meet the demand on the part of district-school teachers and high-school pupils for a simple means of determining the local spring flora.[5] The addition of laboratory hints, outlines of morphology, and directions for the preparation of an herbarium, makes it more than a manual, but its subject-matter is wholly inadequate if it is supposed to comprehend the entire botanical knowledge of the high-school graduate.— J. M. WESTGATE.

AS A COMPANION book to *Our Native Trees* Miss Keeler[6] publishes a similar work on shrubs. The work contains very excellent descriptions of nearly all the native northern shrubs and many common cultivated ones. Accompanying each description is a well-made half-tone illustration of the form. In many instances so good are these figures that they are sufficient to identify the plants. Each description contains many interesting facts about the habits of the shrub. A very simple key is given by which one who is not a professional botanist may identify them. Indeed, the book is intended for the amateur, the lover of nature, and those interested in landscape gardening.— H. N. WHITFORD.

THE LEGUMINOSAE collected in the states of Michoacan and Guerro in Mexico during the years 1898 and 1899 by Eugène Langlassé have been elaborated by the late Marc Micheli.[7] The purpose of Langlassé's exploration was mainly horticultural and the collection of dried plants for the herbarium was purely incidental. Moreover, his collections of all kinds were primarily of the plants having some interest for the horticulturist, or of importance from the point of view of agriculture or forestry. In spite of this, the

[4] HOLTZ, L., Characeen. Kryptogamenflora der Mark Brandenburg, Vol. IV, Part 1. pp. vi + 136. Illustrated. Leipzig: Gebrüder Borntraeger. 1903.

[5] RINGLE, W. E., and KENOYER, L. A., Students' botany of eastern Kansas. 8vo. pp. v + 213. Topeka: Crane & Company, 1903.

[6] KEELER, HARRIET L., Our northern shrubs and how to identify them. 8vo. pp. xxx + 521. *pls. 205. figs 35.* New York: Charles Scribner's Sons. 1903.

[7] MICHELI, MARC, Leguminosae Langlasseanae récoltées dans les états Mexicains de Michoacan et de Guerro pendant les annees 1898 et 1899, par Eugène Langlassé. Mém. Soc. Phys. d'Hist. Nat. Genève 34. 245–294. *pls. 28.* 1903.

number of novelties which M. Langlassé brought back is rather remarkable and indicates the richness of the country in new forms. In the Leguminosae, represented by 237 numbers, M. Micheli finds 26 new species and a new genus, Goldmania, the latter described by Mr. J. N. Rose, of the U. S. National Museum, while many other of the species listed have only recently been published from collections of American botanists. The novelties are illustrated by twenty-eight elegant lithograph plates.—C. R. B.

A CRITICAL ACCOUNT of the algae of northwestern America by Setchell and Gardner[8] has appeared as one of the admirable publications of the University of California. In this paper of 250 pages, with 10 plates, are listed all the known species of algae, excluding the diatoms and desmids, found north of Cape Flattery to the region of Kotzebue Sound in the Arctic coast of Alaska. The authors have had access to a large number of collections, many of them gathered by government parties and other expeditions, and have themselves visited much of the region. They have handled, therefore, probably the largest amount of material ever brought together from this region.

The species are enumerated under the most generally accepted classification, with explicit references to all the specimens examined, and with critical notes on their conditions and peculiarities of structure, habit, and distribution.

A large number of new species and forms are described and figured. Although attention is called to them by printing the names in heavy type, the taxonomic compiler must laboriously pick them out from the main body of the account. A list of these new species properly indexed would have obviated this difficulty.

The authors have refused to change names or upset well-established nomenclature by the application of arbitrary rules, "holding that a name which has been recognized for a quarter of a century, or thereabouts, is to be considered fixed and not to be unsettled simply because another may have been proposed earlier, but hitherto neglected for good or even for no real reasons."—B. M. DAVIS.

NOTES FOR STUDENTS.

KNY[9] finds in three plants (*Lupinus albus*, *Lepidium sativum*, *Vicia sativa*) that diffuse daylight retards the growth in length of soil roots, while darkness is advantageous to it.—C. R. B.

ZEILLER describes[10] the occurrence of species of Zamites, Sphenopteris, and Pagiophyllum, from the Upper Jurassic of the province of Catalonia in

[8] SETCHELL, W. A., and Gardner, N. L., Algae of northwestern America. Univ. Calif. Pub. Bot. 1: 165–418. *pls. 17–27.* 1903.

[9] KNY, L., Ueber den Einfluss des Lichtes auf das Wachsthum der Bodenwurzeln. Jahrb. Wiss. Bot. 38: 421–446. 1902.

[10] ZEILLER, RENE, Sobra algunas impresiones vegetales del Kimeridgense de Santa Maria de Meya. Memor. Real Acad. cienc. y artes Barcelona.

Spain. Two new species, *Pityophyllum flexile* and *Pseudoasterophyllites Vidali*, are likewise figured and described. The first is considered, as the name indicates, to represent fossilized leaves of a species of Pinus. The second after a process of exclusion, the author is disposed to regard as of cupressineous affinities.—E. C. JEFFREY.

IN Comptes Rendus de l'Académie des Sciences, Paris (March 30, 1903), M.C. Queva gives an account of the structure of the rootlets of *Trapa natans*.[11] These are of particular interest because they present the only case known among the phanerogams of a monarchous root. Roots of this type have in the past only been known for the lycopods (unless the rather doubtful case of Ophioglossum be also included), and indeed are almost diagnostic of the radicels of that group.—E. C. JEFFREY.

FROM AN extended study of protoplasmic streaming in plants, carried out by Ewart,[12] it appears that these movements are produced by the energy of surface tension, this being made available perhaps, by the action of electric currents transversing the moving layers. Such currents could be maintained by chemical action in the protoplasm. The movement does not depend directly upon oxygen access, for species of Chara and Nitella continue to exhibit motion for six to eight weeks in entire absence of free oxygen. —BURTON E. LIVINGSTON.

FROM INTERNAL structure and by comparison with specimens having the exterior preserved, Weiss[13] identifies a reproductive branch of a lepidodendroid found near Stalybridge, England, as belonging to the well-known species *Lepidophloios fuliginosus*, and constituting its reproductive branch. The identification is of interest, not only because it reveals the nature of the reproductive main axis of *Lepidophloios fuliginosus*, but also because the axis in question differs from other axes of the genus in having a biseriate instead of a quincuncial arrangement of the cone-scars.—E. C. JEFFREY.

THE curiously modified leaf-members, found in a few living ferns, *e. g.*, *Hemitelia capensis*, but occurring much more commonly in fossil genera, were examined by Potonié[14] from the physiological and morphological standpoints. He concludes that the structures in question are water-absorbing organs, and are specialized pinnae or pinnules as the case may be. The aphlebia or modified pinnae of *Hemitelia capensis* have been compared by

[11] QUEVA, C., Structure des radicelles de la macre. Compt. Rend. Acad. Sci. Paris **136**: 826–7. 1903.

[12] EWART, A. J., On the physics and physiology of protoplasmic streaming in plants. Proc. Roy. Soc. London **69**: 466–470. 1902.

[13] WEISS, F. E., A biseriate halonial branch of *Lepidophloios fuliginosus*. Trans. Linn. Soc. London Bot. II, **6**: 217–235. *pls. 22–26.* 1903.

[14] POTONIÉ, H., Zur Physiologie und Morphologie der fossilen Farnaphlebien. Ber. Deutsch. Bot. Gesells. **21**: 152–164. *pl. 8.* 1903.

Goebel, in regard to their physiological function, with the whole leaf-organ of the Hymenophyllaceae, and the present author suggests that the aphlebia of fossil ferns are to be similarly interpreted.—E. C. JEFFREY.

THE CONDITIONS governing the germination of the spores of the brown rust of bromes (*Puccinia dispersa* Erikss.) have been closely studied by Ward.[15] This rust is an excellent example of a parasite very closely restricted to certain species of hosts, yet forms were found bridging over widely separated sections of the genus. It is interesting to know that these uredospores retain their vitality for long periods, month-old spores germinating readily, and certain forms after sixty-one days. But the conditions governing the germination of uredospores are very uncertain, for there are internal factors, such as the age of the spore-bearing mycelium and degree of ripeness, beside the external factors of temperature, aeration, moisture, etc.—B. M. DAVIS.

PALLADINE AND KOMLEFF[16] have determined that the respiratory energy of cut etiolated leaves of *Vicia faba* placed in solutions of cane sugar is greatest when the solution has a concentration of about 5 per cent. This fact seems not to depend upon sugar assimilation, for the latter increases with the concentration at least as far as a 20 per cent. solution, the highest concentration tested. But the respiratory energy is greatest when there is the largest amount of insoluble proteid substances present in the leaves, a condition attained in a 5 per cent. solution of cane sugar. When the leaves are transferred from one concentration to another respiration is augmented with decrease and diminished with increase of concentration. This supports the view that foods are not directly consumed in respiration.—BURTON E. LIVINGSTON.

"THE AECIDIUM as a device to restore vigor in the fungus" is the subject of a short discussion by Professor Arthur,[17] who believes that the aecidium with the accompanying spermogonia represents the original sexual stage of the rust. It appears that wheat infected from aecidial spores will produce teleutospores (black rust) much more quickly than if the infection be through uredospores, and it is well recognized that the black rust is more injurious to the wheat than the red rust. Hence the author regards the aecidiospore as more virile than the uredospore, since it produces a more vigorous and harmful parasite. The question, however, suggests itself whether this added virility has really any connection with the organ called the aecidium. It is possible

[15] WARD, H. M., Further observation on the brown rust of the bromes, *Puccinia dispersa*, and its adaptive parasitism. Ann. Mycol. 1: 132–151. 1903.

[16] PALLADINE, W., and KOMLEFF, A., L'influence de la concentration des solutions sur l'énergie respiratoire et sur la transformation des substances dans les plantes. Rev. Gén. Bot. 14: 497–516. 1902.

[17] ARTHUR, J. C., The aecidium as a device to restore vigor to the fungus. Proc. Soc. Prom. Agric. Sci. 23: 1–4. 1903.

that the mere change of host (wheat to barberry and back to wheat) may give to the rust that variety of life conditions which is generally beneficial to every organism, in contrast to monotony of food and environment.— B. M. DAVIS.

IKENO[18] has continued his studies on spore formation in Taphrina which were first reported in Flora 88:229. 1901. He finds essentially the same conditions in several species that he described for *Taphrina Johansoni*. There is always the fusion of two nuclei in the ascus preliminary to spore formation. The chromatin material in the fusion nucleus may split up into a number of fragments, which become scattered in the cytoplasm by the dissolution of the nuclear membrane and organize very small nuclei. Or, division may proceed more regularly through successive halving of the chromatin, sometimes accompanied by simple mitotic phenomena. There is generally at the end extensive multiplication of the nuclei by fragmentation and division of the spores by budding. No asters were discovered to cut out the spores as in the higher Ascomycetes, but the cytoplasm seems to gather more densely around the nuclei and form the spore wall. There is no evidence in the ascus of cleavage by constriction.— B. M. DAVIS.

THE LARGE PROPORTION of the seeds of the darnel (*Lolium temulentum*) are infected with a fungus which causes the development of a substance (lolium) with toxic effects upon man and certain carnivorous animals, but not injurious to pigs, cattle, or geese. This interesting parasite has been recently studied by Freeman.[19] No spores are known, and the fungus apparently passes from one generation of the host to the next with the seed. It does not appear to harm the darnel; on the contrary, the infected seeds seem to be larger and better developed than those free from the fungus. Infected seeds germinate very well. There is, therefore, the possibility of an advantage to the host, but this is not positively known. The relationships of the fungus have been much discussed, but in default of spore fructifications the conclusions are mere speculations. The invasion of the young seedling from the coats of the seed and the later appearance on the ovaries is smut-like, but there are also points of resemblance to ergot, and especially to an ergot that frequently attacks Lolium in England.— B. M. DAVIS.

A MEMOIR on Todea, of the same admirable character as former works of the senior author on ferns possessing at the same time fossil and living representatives, is published by Seward and Ford.[20] The anatomy of the mature stem of *Todea barbara*, *T. superba*, and *T. hymenophylloides* is

[18] IKENO, S., Die Sporenbildung von Taphrina-Arten. Flora 92:1–31. *pls. 1–3*. 1903.

[19] FREEMAN, E. M., The seed-fungus of *Lolium temulentum* L., the darnel. Phil. Trans. Roy. Soc. London B. 196:1–27. *pls. 1–3*. 1903.

[20] SEWARD, A. C., and FORD, SYBILLE O., The anatomy of Todea with notes on the geological history and affinities of the Osmundaceae. Trans. Linn. Soc. London Bot. II. 6:237–260. *pls. 27–30*. 1903.

described. The results of Faull in the two former species are in the main confirmed. The last species is of interest because, like *Osmunda cinnamomea*, it has an internal endodermis surrounding the pith in the adult; but unlike the latter this does not appear in the young axis. The figures and description of the authors leave some room for doubt as to the entire accuracy of of this statement, for they do not follow the central cylinder to a sufficient height in the sporeling to exclude their having missed the first appearance of the internal endodermis. An admirable résumé of the fossil Osmundaceae is given, from which it appears how unsatisfactorily meager is our knowledge of this interesting group of ferns, particularly on account of the paucity of specimens from the Mesozoic.—E. C. JEFFREY.

VARIOUS PERIODIC phenomena in connection with the growth and development of plants are well known. Many of these depend upon conditions at present wholly unknown and are designated, therefore, as autonomous. As illustrations may be cited the grand period of growth, the variation in the length of internodes and often of interfoliola (by which Münter long ago designated the spaces between the pinnules on the common petiole). Tammes[21] has endeavored to determine the influence of the presence or absence of leaves upon some of these periodic phenomena. Thus he finds that if all leaves be removed from an annual shoot the periodicity in the length of the internodes is not disturbed, the elongation of the cells only being interfered with, so that the internodes remain shorter than in the living shoot. But the removal of one or more leaves does disturb the periodicity. Certain internodes have less length than in the normal shoots. One would expect that each leaf would affect only the growth of those internodes adjacent to it, but this is not the case, internodes above as well as below the removed leaves being influenced. Often more strikingly than the annual shoots the interfoliola show a similar effect from the removal of leaflets.—C. R. B.

LIDFORSS[22] has investigated the geotropic response of some spring plants whose geotropism is influenced by variations of temperature. These are almost exclusively plants which conclude their development before the warm season. He finds that many of these shoots at lower temperatures are diageotropic, while at higher temperatures they are apogeotropic. This he considers a typical case of dynamic anisotropism. Somewhat similar reactions, however, may be due to changes in temperature alone. In general those shoots whose geotropic reactions are influenced by alterations of temperature are more or less epinastic at lower temperatures, but this epinasty, which reaches its maximum a little above zero, disappears completely at temperatures above 20 degrees. At low temperatures darkness may also affect

[21] TAMMES, T., Die Periodicität morphologischer Erscheinungen bei den Pflanzen. Verhandl. Konigl. Akad. Wetens. Amsterdam. II. 9: no. 5. 1903.

[22] LIDFORSS, B., Ueber den Geotropismus einiger Frühjahrspflanzen. Jahrb. Wiss. Bot. 38: 343–376. *pl. 3.* 1902.

geotropic reactions, so that shoots diageotropic in light become apogeotropic in darkness.

Lidforss holds that the term "psychrocliny," introduced by Vöchting, includes a series of phenomena which doubtless have the same ecological importance, but are in no wise equivalent physiologically. Unless the term be reserved as a physiological one for those cases in which temperature actually produces a modification of the geotropism, he thinks it should be abandoned.—C. R. B.

A NUMBER of Bulletins of the United States Agricultural Department deserve brief mention.

VON SCHRENK[23] discusses among other subjects the relation of water to the decay of timber, how timber is seasoned, seasoning tests with lodgepole pine and oak, and tests with telephone poles.

GRAVES AND FISHER[24] treat of the woodlands of southern New England. Improvement cuttings, reproduction cuttings, platting, pruning, protection of the woods and other subjects are well handled.

In another bulletin VON SCHRENK[25] has investigated the cause of the blue color of dead wood in *Pinus ponderosa* (which he finds due to the blue fungus, *Ceratostomella pilifera* (Fr.) Winter), the effect of coloring on the value of the wood, the reason for the decay of wood and how prevented, and whether it would be possible to use the dead wood before it decays. The bark beetle (*Dendroctonus ponderosae*) spreads the fungus, therefore it is recommended that the dead wood be removed at once, for standing beetle-infested trees serve to spread the insect.

HERTY[26] shows that an improved method of turpentine orcharding will increase profits sufficiently to warrant its adoption by any turpentine operator.—H. N. WHITFORD.

VAN WISSELINGH, in his earlier papers upon karyokinesis in Spirogyra, devoted his attention to the nucleolus and the nuclear net-work. In the fourth paper[27] of the series he deals with the nuclear membrane, the spindle, and the walls of the vacuole. *Spirogyra triformis*, a species with thin walls

[23] VON SCHRENK, HERMANN, assisted by HILL, REYNOLDS, Seasoning of timber. Bull. No. 41. Bureau of Forestry, U. S. Dept. of Agric. pp. 48. *pls. 28. figs. 16.* 1903.

[24] GRAVES, H. S. and FISHER, R. T., The woodlot: a handbook for owners of woodlands in southern New England. Bull. No. 42. Bureau of Forestry, U. S. Dept. of Agric. pp. 89. *pl. 4. fig. 30.* 1903.

[25] VON SCHRENK, HERMANN, The "bluing" and the "red rot" of the western yellow pine, with special reference to the Black Hills forest reserve. Bull. No. 36. Bureau of Plant Industry. U. S. Dept. of Agric. pp. 40. *pls. 14.* 1903.

[26] HERTY, C. H., A new method of turpentine orcharding. Bull. No. 40. Bureau of Forestry, U. S. Dept. of Agric. pp. 43. *pls. 15. figs. 5.* 1903.

[27] WISSELINGH, C. VAN, Untersuchungen über Spirogyra. Vierter Beitrag zur Kenntniss der Karyokinese. Bot. Zeit. **60**: 115–138. *pl. 5.* 1902.

and loose, delicate chromatophores, was chosen for study. Material was fixed in Flemming's solution and afterward treated with a strong solution of chromic acid (40 per cent.), which dissolved successively the cytoplasm, karyoplasm and nucleolus, but did not dissolve the spindle fibers. Sections do not seem to have been used.

During the earlier stages of karyokinesis the nuclear membrane is entirely resorbed. The spindle is derived from the granular cytoplasm about the nucleus and consists of but one kind of fibers, the two different lengths of fibers and the two opposite groups described by Strasburger for *Spirogyra polytaeniata* not appearing in *S. triformis*. The spindle fibers do not grow through the nuclear membrane as described by Strasburger. The spindle is at first multipolar, but becomes bipolar. There is no diminution in the number of spindle fibers during karyokinesis, but after karyokinesis the spindle fibers become resolved into cytoplasm. The spindle fibers resist the action of chloral hydrate and so are easily distinguished from cytoplasmic strands. The walls of the vacuoles are also made visible by chloral hydrate. During karyokinesis the walls of the vacuoles with some cell sap press between the spindle fibers and appear within the spindle. Between the two halves of the nuclear plate a number of plasma strands are formed inclosing the spindle fibers, but there is no persistent, closed connecting tube as described by Strasburger for *S. polytaeniata*.—CHARLES J. CHAMBERLAIN.

A NUMBER of fossils, brought together by the late Sir William Dawson, have been described by Penhallow.[28] The first lot are from the Lower Cretaceous of Queen Charlotte islands, and the Upper Cretaceous of Port McNeil, Vancouver island. Several ferns are described, among them a new species, *Osmundites skidegatensis*, from Skidegate Inlet, Queen Charlotte islands, which is referred to at length in connection with a fuller subsequent description. Of gymnosperms there are species of Cycadites, Zamites, Ginkgo, and Sequoia. In *Sequoia langsdorfii* (Brongn.) Heer, the wood is described for the first time, although the foliage and fruit have long been known. The wood is of special interest because like that of *S. sempervirens*, the living species which so closely resembles *S. langsdorfii*, otherwise, it contains resin-canals such as are in general confined to the woody tissues of the Abietineae. The second lot of material is from the early Eocene of Blind Man river, N. W. T. of Canada, and includes a number of ferns, an Equisetum, and several gymnosperms. Several monocotyledonous and dicotyledonous species are also described and figured.

In another paper[29] Penhallow gives a fuller description of the fossil *Osmundites skidegatensis*, mentioned in the article referred to above. The

[28] PENHALLOW, D. P., Notes on Cretaceous and Tertiary plants of Canada. Trans. Roy. Soc. Canada II. **8**: 31–91. 1902.

[29] PENHALLOW, D. P., Osmundites skidegatensis. Trans. Roy. Soc. Canada II. **8**: 3–30. 1902.

account is based on the study of material collected by Dr. F. C. Newcombe from Alliford Bay, Skidegate Inlet, Queen Charlotte islands, and is illustrated by a number of photographs and photomicrographs, which testify to the admirable preservation of the fossil. The author concludes that the fossil represents a plant of the general habit of *Osmunda regalis*, but is much larger than any of the species of that genus found in North America. Internally it resembles Osmunda on the one hand and Todea on the other; but the resemblance seemed on the whole to be closer to Osmunda than Todea, so the fossil is included by the author in the genus Osmundites.—E. C. JEFFREY.

HABERLANDT sums up the present data of the statolith theory of geotropic preception,[30] prefacing his paper with a short historical account of the development of the same theory for animals. He answers certain objections which have been raised and contributes some new support to the theory, which now seems reasonably established for a considerable number of plants. Starch-bearing cells of the root cap in roots and of the starch sheath in stems (which is present in the majority of phanerogams, although Fischer, investigating too old portions of the stem, found it often wanting) are the preceptive organs, except in certain cases, where the geotropism is limited to the nodes, or where sharply differentiated groups of cells with movable starch grains replace the absent starch sheath. The preceptive apparatus is found to have degenerated in stems which have lost their geotropic sensitiveness, and to be lacking in organs which show no reaction to gravity. In general the root caps of apogeotropic climbing roots either contain no starch grains or non-motile ones. In orthotropous organs the protoplasmic membranes next the lower and upper transverse walls of the preceptive cells are not sensitive; only the membranes of the tangential longitudinal walls are irritable, and especially that of the outer wall in apogeotropic organs and that of the inner wall in positively geotropic organs. Whether both tangential walls of the same cell are sensitive is uncertain. In the nodes of grasses there is no ground for admitting this. The protoplasmic membranes on the radial walls are probably not sensitive. Any process which removes the starch from the starch sheath at the same time stops geotropic response, which, however, may begin again when the starch is regenerated. Czapek's demonstration of this in roots, from which starch disappeared when they were inclosed in plaster casts, is now supplemented by Haberlandt's experiments in removing starch by subjecting plants to low temperatures and then bringing the protoplasm into a condition of sensitiveness by raising the temperature. Until some hours have elapsed and starch grains have begun to appear, the geotropic sensitiveness does not manifest itself. Further experiments show that the action of gravity as a stimulus rests upon the static pressure of solid bodies. Further-

[30] HABERLANDT, G., Zur Statolithentheorie des Geotropismus. Jahrb. Wiss. Bot. **38**: 447–500. *fig. 3.* 1902.

more the time occupied by the fall of the starch grains through the cell fluids to the new position, which may be designated as the migration time, is shown to be usually less than half the presentation time. The migration time may be diminished by repeated mechanical jarring, in which case the presentation time is correspondingly diminished. It seems probable to the reviewer that subjecting plants to centrifugal action might reduce the migration time to a minimum and so demonstrate more clearly this relation.—C. R. B.

THE SEXUAL ORGANS and the development of the ascocarp of Monascus are described by Barker[31] in a paper of especial interest in relation to the problems connected with coenogametes among the Phycomycetes and Ascomycetes. A filament develops terminally an antheridium. Immediately below this cell the ascogonium is formed, whose growth pushes the antheridium to one side. Both sexual organs are multinucleate (coenogametes). They fuse by means of a small process put forth from the antheridium. After fertilization the ascogonium becomes divided by a cross wall, the anterior small cell remaining in connection with the antheridium, and the posterior, named the "central cell," developing the ascocarp.

After fertilization the central cell becomes invested by a growth of hyphae from below. The central cell now increases greatly in size, and the next change is the development of ascogenous hyphae in a little depression at one side of the central cell. The ascogenous hyphae gradually fill the interior of the ascocarp, eventually forming small eight-spored asci. The central cell plays a curious part in the later developments of the ascocarp. The growth of the ascogenous filaments so presses upon it as to force its wall inward, giving it the shape of a bowl. The ascogenous hyphae thus appear as an internal development, but their origin is plainly external. Later the contents of the central cell disappear, and its walls become cutinized, so that they actually form a hollow sphere around the ascogenous hyphae. Since the latter break down with the ripening of the spores, the mature ascocarp has the appearance of a simple sporangiumlike structure, which it is not.

Barker regards Monascus as a very lowly ascomycete, with relationships rather nearer to the Gymnoascales than to any other group. A number of points in his general discussion are treated in a note that follows my paper on Oogenesis in Saprolegnia.[32]—B. M. DAVIS.

[31] BARKER, B. T. P., The morphology and development of the ascocarp in Monascus. Ann. Bot. **17**: 167–236. *pls. 12, 13.* 1903.

[32] BOT. GAZ. **35**: 344. 1903.

NEWS.

DR. M. WESTERMAIER, professor of botany in the University of Freiburg, died on May 1.

DR. J. M. GREENMAN has been promoted to an instructorship in botany at Harvard University.

DR. JOSEPH E. KIRKWOOD, instructor in botany in Syracuse University, has been promoted to an associate professorship.

DR. C. ARTHUR HOLLICK will spend the summer in Alaska in paleobotanical investigations under the auspices of the U. S. Geological Survey.

AT THE June convocation the University of Chicago conferred the degree Ph.D. upon three candidates in botany, Harry N. Whitford, George M. Holferty, and John F. Garber.

DR. RAYMOND H. POND has been appointed professor of botany and pharmacognosy and director of the microscopical laboratories of the School of Pharmacy of Northwestern University.

M. FR. CRÉPIN, the director of the Royal Botanical Garden at Brussels, died April 30, at the age of seventy-two. He has been incapacitated for more than a year by illness. M. Th. Durand, the curator of the herbarium, has been appointed director.

THE WORK on *Pteridophyta* and *Spermatophyta* of Southern California, by Samuel B. Parish, which the Southern California Academy of Sciences proposed two years ago to publish as volume II of its Proceedings if a sufficient number of subscribers could be obtained, will not be published on account of lack of support for the undertaking.

DR. GUSTAV RADDE, imperial councilor and director of the Caucasian Museum, died recently at Tiflis at the age of seventy-one. He has been widely known as a student of the oriental flora. One of his last important works was *Grundzüge der Pflanzenverbreitung in den Kaukasusländern*, reviewed in this journal in April 1902.

ON APRIL 10, at the age of seventy-five, the venerable mycologist, Dr. Andreas Allescher, died suddenly of apoplexy at Munich. On retiring from active teaching in the Königl. Kreis-Lehrerinnen-Seminar he devoted the last five years of his life to the elaboration of the Fungi Imperfecti for Rabenhorst's *Kryptogamen-Flora*, a task which happily he completed before his death.

THE FORMAL OPENING of the new Lake Laboratory building of the Ohio State University, recently erected at Cedar Point, Sandusky, Ohio, took place Thursday, July 2, 1903. Addresses were given by Professor C. J.

Herrick, of Denison University, President of the Ohio Academy of Sciences; by members of the Board of Trustees and of the Faculty of the University; and by Professor Herbert Osborn, Director of the laboratory.

SCIENCE announces that Professor F. E. Lloyd, of Teachers College, Columbia University, left June 13, by the steamer "Caribee," for the island of Dominica, where, in the company of Mrs. Lloyd, he will spend the summer in the study of the flora. The expedition is under the auspices of the New York Botanical Garden, and the systematic collections will become a part of the garden herbarium. Professor Lloyd has received a grant of $200 from the Esther Herrman research fund of the Scientific Alliance of New York, to aid him in the collection of tropical Rubiaceae to be used in the furtherance of his researches in the embryology of that order.

IN APRIL 1903 appeared volume 1, number 1, of a monthly quarto review, entitled *Flora and Sylva*. The aim of this periodical is to illustrate in color and by good engravings new, rare, or valuable herbaceous plants, trees, and shrubs, fitted for the English climate, and to show appropriate and picturesque planting of grounds and garden design. The typography and paper are sumptuous; the colored plates, two in this number, are well executed chromo-lithographs. The illustrations in black are apparently wood engravings, the character of the paper preventing the use of half-tones. In this number articles on the hardy bamboos in England, on new daffodils, on the genus magnolia, and a revision of the genus Calochortus, with shorter articles on a variety of subjects indicate the general scope of the journal. The editor is Mr. W. Robinson, the author of *The English flower garden*. *Flora and Sylva* promises to be a worthy addition to the horticultural literature of our day. No yearly subscription price is indicated; but the single number is marked "price half-a-crown."

THE REPORT of the officers of the New York Botanical Garden for 1902 shows that the number of herbaceous species grown in the Garden is about 3000. Grading operations and making of paths have still interfered with the extension of the planting of shrubs and trees, but the fruticetum contains over 530 species, the salicetum about 50 species, the arboretum about 300 species, and the viticetum about 60 species. A great increase has been made in the collections of plants cultivated under glass, which now number nearly 6000 species. The approach to the museum building and the public conservatory were completed during the year. The library has increased by nearly 2000 volumes and now consists of about 13,000 bound volumes. 67,000 specimens have been recived for the museum and herbarium. Forty-three students, including graduates of thirty-one different colleges and universities have been granted the privileges of the museum, library, and laboratories during the year, in addition to numerous visiting investigators from other institutions. Many explorations have been carried out by members of the staff, to which over $4000 has been devoted. The report is an interesting account of the progress of this great institution.

VOLUME XXXVI NUMBER 2

BOTANICAL GAZETTE

AUGUST, 1903

STUDIES IN SPINDLE FORMATION.

ANSTRUTHER A. LAWSON.

(WITH PLATES XV AND XVI)

HISTORICAL.

THE evidence produced from the researches of the last few years[1] proves quite conclusively that a centrosome as a spindle-forming organ does not exist in the higher plants. Too few forms, however, have been worked out in sufficient detail to allow of any definite conclusions as to whether or not these plants have any common uniform method of spindle formation. Of the types that have been thoroughly examined, the following have been recorded:

In 1897 Osterhout investigated the spindle in the spore mother-cells of Equisetum. The first indication of a spindle in these cells is the formation of a felted zone of kinoplasmic fibers surrounding the nucleus. These fibers grow out from the nuclear membrane and assume a radial position. By the fusion of their free ends these fibers form a series of cones, and upon the breaking down of the nuclear membrane the cones unite at their apices in two groups to form the bipolar spindle.

In 1898 the writer investigated the development of the spindle in the pollen mother-cells of Cobaea. Here it was found that, as division approaches, a dense granular cytoplasmic substance

[1] Belajeff (1894), Byxbee (1900), Davis (1899, 1901), Debski (1897), Farmer (1893, 1895), Guignard (1898), Juel (1897), Lawson (1898, 1900), Mottier (1897 *a*, *b*,) Němec (1898, 1899), Osterhout (1897, 1902), Smith (1900), Strasburger (1896, 1897, 1900), Webber (1897), Weigand (1899), Williams (1899).

forms a complete zone about the nucleus. The nuclear wall disappears, and the central part of the cell becomes filled with a network of kinoplasmic fibrils, in which the chromosomes lie. This network grows out into several projections, which become the primary cones of the multipolar spindle. These cones now unite at their apices into two groups and thus form the bipolar spindle.

In 1899 Williams describes for Passiflora a process somewhat resembling that which occurs in Cobaea. Upon the breaking down of the nuclear wall, there is a large kinoplasmic network formed in the central portion of the cell. This network of fibrils projects outward at various points and becomes cones, which, uniting at their apices in two groups, form the mature spindle.

In 1900 the writer investigated the spindle in Gladiolus. Here, as in Equisetum, the first indication of the spindle in the mother-cell is the formation of a felted zone of kinoplasmic fibrils surrounding the nucleus. But instead of the fibrils taking on a radial arrangement, as described for Equisetum, the zone grows out at irregular intervals in the form of sharp pointed projections, which are the primary cones of the spindle. The nuclear wall remains intact until the cones are fully developed, and upon its breaking down the cones collect by the fusion of their apices into two groups, when the bipolar condition is reached.

Byxbee (1900) has recorded the following method for the development of the spindle in the pollen mother-cells of Lavatera. The meshes of the network close to the nuclear wall pull out in a direction parallel to the wall, forming a felt of fibrils about the nucleus. The cytoplasm now collects in a dense granular zone about the nuclear membrane, as it does in Cobaea. Upon the breaking down of the nuclear wall, there is formed a central mass of fibrils in which the chromosomes are suspended. This central mass of fibrils grows out into several projections, bringing about the multipolar condition of the spindle. Two of the cones become more prominent than the others, which they absorb, and the bipolar figure is thus produced.

Smith (1900) has worked out with considerable detail the

development of the spindle in the spore mother-cells of Osmunda. In this case the spindle originates from a zone of kinoplasm which surrounds the nucleus. The granules in the kinoplasm arrange themselves in rows, concentric with the nuclear wall, and are finally massed on opposite sides of the nucleus. From these masses two cones of fibrils are developed, which become the two cones of the spindle. As there are only two primary cones developed, the spindle is bipolar from the first.

Osterhout (1902), in his recent work on Agave, records the following series of events leading to the formation of the spindle in the mother-cell. During the early stages there is developed a cytoplasmic membrane outside of the nuclear wall. This he calls the "spindle membrane," and he regarded it as a unique structure. There is no weft of fibrils formed, but the spindle-forming fibrils are radial from the beginning, and are attached to both the nuclear and spindle membranes. From these radial fibrils the cones are developed, and these, by fusing into two groups, bring about the bipolar condition. Probably the most remarkable observation that Osterhout has recorded is that the second spindle formation differs entirely from the first. According to his observations, the spindle-forming fibrils of the second division are found in close contact with the nuclear wall, and their free ends radiate from it. They extend outward into the cytoplasm, and by the union of their ends form a series of cones. These fuse at their apices into two groups and form the bipolar spindle in much the same fashion as in Equisetum.

From the observations of the writers described above it is perfectly obvious that there are considerable differences between the methods of spindle formation. It is also evident that there are certain important features which are common to nearly all of them. It would seem that there are several distinct types of spindle formation, but the differences between them are too great, and the number of forms worked out in detail are too few to allow of any generalizations. The number and character of these types can be determined only by additional observations. It is to this end that the following studies are recorded.

METHODS.

These were essentially the same as those used in my work on Cobaea and Gladiolus. As full details are recorded in these papers, it will be unnecessary to repeat them. It is only necessary to add that the material was all fixed in the field, and by far the most satisfactory results were obtained by using Flemming's weak solution of chromic-osmic-acetic acid as a killing agent, and the triple stain, safranin, gentian, and orange G.

THE POLLEN MOTHER-CELLS OF IRIS FLORENTINA.

The young anthers of the common garden Iris furnish very good material for the study of spindle formation. If conditions are favorable and the material is fixed in the field, immediately after being detached from the plant, all the stages in the formation of the spindle of the first division of the pollen mother-cells may be observed in a single anther. As the anthers at this stage are very large, many sections may be obtained from one of them. Previous to the formation of the first spindle, the nucleus of the mother-cell is very large, containing one or two nucleoli and the chromatin thread. The cytoplasm appears to be a reticulum, the threads of which are more or less granular. In the immediate neighborhood of the nuclear wall, the cytoplasm is more dense than at the periphery, but this dense region is not as sharply differentiated as that described by the writer for this stage in the pollen mother-cells of Cobaea and Gladiolus. Numerous small spherical bodies, probably oil globules, were found distributed irregularly through the cytoplasm.

While the chromatin is yet in the spirem stage, the cytoplasm immediately in contact with nuclear membrane becomes differentiated into a distinct weft or felted zone of fibrils. This weft appears at first to consist of a few delicate but very distinct fibrils, which stain blue with the gentian violet, in contrast to the slightly orange color of the rest of the cytoplasm. They do not radiate from the nuclear membrane, but lie more or less parallel to it. When followed along their course, they were found to lose gradually their affinity for gentian violet, and to terminate in the regular orange-colored threads of the cytoplasm. This indicates

that the kinoplasmic threads are nothing more than modified threads of cytoplasm, which have lost their reticulated and granular character and have become more distinctly thread-like. *Fig. 1* shows one of the early stages in the formation of the weft, which ultimately develops into the spindle. Even in stages earlier than this, the fibrils were sharply differentiated, both in their structure and staining properties, from the surrounding cytoplasm. The fibrils gradually increase in numbers, evidently at the expense of the reticulum of the cytoplasm, and soon a fibrous zone of considerable thickness completely surrounds the nuclear membrane *fig. 2*. As far as the development of this zone is concerned, the process is identical with that which occurs in Gladiolus (Lawson, 1900). In Gladiolus, however, the chromosomes were already formed when the weft was developing, while in Iris the chromatin is yet in the spirem stage.

Fig. 2 shows the appearance of the fibrous zone when fully developed. Up to this time it increased in thickness almost uniformly, but it now grows outward at irregular intervals. Two of these outward projections are shown in *fig. 2*. The meshes formed by the interlacing fibrils of the weft become elongated in the directions in which the fibrils are growing, that is, in the direction of the projection. These outgrowths of the fibrous zone are the first indications of the primary cones of the so-called multipolar stage of the spindle, and the threads composing them converge toward their apices.

During the development of the cones the chromatin assumes the form of distinct chromosomes, and the nucleoli become vacuolated.

The development of the cones is not only brought about by the pushing out of the original weft at certain intervals, but they apparently increase at the expense of the cytoplasm into which they project. *Fig. 3* shows one of the cones projecting into the cytoplasm, and the outermost fibrils converging to its apex are continuous with the fibrils of the cytoplasmic reticulum. *Fig. 4* shows the cones at a later stage; the larger cone is much more sharply defined. It has lost much of its reticulated appearance, and its fibrils are more independent of one another, except

where they converge at the apex. There is apparently no definite position for the projection of each cone. They may be separated by considerable distance, or again there may be two or three quite close together (*figs. 5, 6*). The number also seems to vary, although there are always more than two formed. Cross sections always show three or four. *Fig. 6* shows three on one side, and an indication of a fourth on the opposite side of the nucleus. This figure also shows that the growth of the various cones is not simultaneous.

One of the striking features of the cones is the remarkably sharp point with which each one terminates. These sharp-pointed apices extend outward as the fibrils composing the cones elongate, and they indicate the outermost points at which are taking place the changes which bring about the transformation of the cytoplasmic reticulum into spindle-forming fibrils.

As in Gladiolus, the nuclear membrane persists until the cones have almost attained their maximum development. In *fig. 7* a portion of the nuclear wall remains, and several of the cones have fused together before the nuclear membrane entirely disappears. This fusion, however, probably does not begin until the nuclear wall begins to break down. When this is accomplished the chromosomes become attached to the fibrils at the base of the cones. During and after this stage the collecting together of the cones was very noticeable.

By the time the nuclear wall has entirely disappeared, and all the chromosomes are connected with the fibrils, the cones unite at their apices into several groups (*fig. 8*). Here three of these groups are represented, which are the product of the union of several primary cones. The space that was occupied by the nuclear sap is now filled with a complex of delicate fibrils, and all of the chromosomes are connected with fibrils which extend to the apex of one or other of the cones. By further union of the cones (*figs. 9, 10*), the number of cone aggregates is reduced to two. Up to and including the stage represented in *fig. 9*, the fibrils composing the cones were of the same general character, but in the following stages there is a differentiation of the fibrils, according to the part they take in the mature spindle. We have,

for instance, those that are connected with the chromosomes, those that extend from end to end of the spindle, and those that extend laterally outward with their free ends projecting into the cytoplasm. These are known as the connective, continuous, and mantle fibers respectively.

The spindle having now reached the bipolar condition, and the connective fibrils from the respective poles having become connected with the chromosomes (*figs. 10, 11*), the latter bodies take up their characteristic position at the equator, and the formation of the spindle is complete.

The series of events leading to the formation of the spindle, as here described for Iris, agrees in every essential detail with those which occur in Gladiolus.

THE POLLEN MOTHER-CELLS OF DISPORUM HOOKERI.

The anthers and pollen mother-cells of Disporum are not as large as many other liliaceous types that have been used for the study of spindle formation ; nevertheless, they form an extremely interesting subject. When properly fixed in the field, the various stages in the formation of the first spindle of the mother-cell may be readily obtained.

In the resting condition of the mother-cell, the nucleus is centrally situated, but as division approaches it is invariably found near one side. Before any kinoplasmic differentiation takes place, the chromatin has broken up and assumed the form of definite spherical chromosomes, of which there are but eight. The first evidence of spindle formation is to be found in the transformation of the cytoplasm in the immediate vicinity of the nuclear membrane. At first, this change takes place in much the same manner as described above for Iris. There are in the beginning but a few short threads, which when followed outward are found to be continuous with the reticulum of the surrounding cytoplasm, but they have lost the granular character and stain blue with the gentian violet. These threads increase in number and gradually form a distinct weft, which appears to form more abundantly on one side of the nucleus than on the other; that is, it is much more evident on the side

of the nucleus farthest away from the cell wall (*fig. 12*). While the beginning of the weft resembles that described for the stage in Iris, it soon takes on a very different form as it increases in size. Instead of the meshes running more or less parallel to the membrane of the nucleus, they elongate more at right angles to it (*figs. 12, 13*). The fibrils composing the weft stain deep blue, while the peripheral cytoplasm stains slightly orange. If, however, we follow the individual fibrils outward, they gradually lose their property of staining blue and stain slightly orange. They are, in fact, strictly continuous with the more granular threads of the cytoplasmic reticulum. They therefore seem to be nothing more than transformed threads of cytoplasm.

As already stated, the growth of the weft is not uniform; it is much more conspicuous on one side of the nucleus than on the other. This irregularity is carried still farther as the weft increases in size. The meshes elongate much more, the individual fibrils which form them lengthen considerably, and their individuality becomes much more pronounced. As the weft now increases, it does so by several projections, which terminate in sharp points, so that we have distinct cones formed (*fig. 14*), in much the same manner as they are formed in Iris. These cones at first vary considerably in number and size, and are invariably much more numerous on the side of the nucleus away from the cell wall (*fig. 14*). From a careful study of the development of these cones as they project into the cytoplasm, there seems to be little doubt that the fibrils composing them are transformed directly out of the reticulum of the cytoplasm. This is particularly evident in the earlier stages, where there is no sharp differentiation between the ends of the fibrils of the weft and the surrounding threads of cytoplasm, the one passing into and apparently being continuous with the other.

As the cones project outward, they terminate in very sharp points and extend over half way to the cell wall opposite (*figs. 14, 15*). During the entire process of their development the nuclear membrane and the nucleolus persist. There is no evidence of the breaking down of these structures until the cones are fully developed. As soon as the cones cease growing out-

ward, the nuclear membrane disappears rapidly, and the ends of the fibrils at the base of the cones become attached to the chromosomes.

The sequence of events which leads to the bipolar condition of the spindle is essentially the same as that described for Iris. Upon the breaking down of the nuclear membrane the apices of certain of the cones move toward each other and form several groups of cones. These in turn unite still further, until we have the characteristic so-called multipolar spindle. *Fig. 16* shows a stage approaching the bipolar condition. The connective fibers which attach themselves to the chromosomes become more sharply defined than the other fibrils, and appear to be thicker in the region of the chromosomes, as if they had already begun to contract. By the time the chromosomes have arranged themselves at the equatorial plate, the cones have united into two groups, which are the poles of the bipolar spindle. The mature spindle does not show the free mantle fibers which are so characteristic of Cobaea, Gladiolus, Iris, and many other forms. There are a few delicate continuous fibrils, which extend from pole to pole. The connective fibrils are much coarser than the continuous ones, stain more deeply, and are much more clearly defined. In the bipolar stage of the spindle, these fibrils appear to be much thicker in the region of the chromosomes, which suggests that they have not begun to contract, but that the chromosomes imparted the stimulus to contract. This condition of the fibrils is shown in *fig. 17*.

As the chromosomes (eight in polar view) approach the poles, the connective fibrils shorten and thicken, and by the time they have reached the poles the connective fibrils have disappeared entirely; the continuous fibrils, however, have increased in numbers. Having reached the poles, the chromosomes unite and form a mass of chromatin at each end of the spindle. Nuclear sap is now secreted, and a membrane is formed about each daughter nucleus.

The daughter nuclei are small, and the various stages in the development of the spindle of the second division were difficult to follow. The early weft stage, however, was observed, as well

as the later multipolar stages, which show clearly that the process of spindle formation in the second division is essentially the same as in the first.

THE POLLEN MOTHER-CELLS OF HESPERALOE DAVYI.

As in Iris and Disporum, the first indication of spindle formation in the pollen mother-cells in Hesperaloe is the differentiation of the cytoplasm in the immediate neighborhood of the nuclear wall into a distinct weft of fibrils. This weft is very small at first, but as it stains blue very readily when the triple stain is used, it can be clearly distinguished. The fibrils run almost parallel with the nuclear membrane, even at the beginning of their formation, and they keep this position until the weft has reached a considerable thickness. In this respect it is almost identical with Gladiolus and Iris, but differs slightly from Disporum. *Fig. 18* shows the weft fairly well developed. It encreases uniformly and completely surrounds the nuclear membrane. As in Iris and in Disporum, there is no sharp differentiation between the outer fibrils and the reticulum of the surrounding cytoplasm. It would seem that the cytoplasm loses its granular structure, becoming more distinctly threadlike, with meshes parallel to the nuclear wall, and stains blue instead of orange.

Following the same series of events that occur in Gladiolus, Iris, and Disporum, the weft soon ceases its uniform growth and proceeds to grow out at irregular intervals in the form of pointed projections. The meshes of the weft in these outward growths are no longer parallel to the nuclear membrane, but are elongated in the direction of the projections. *Fig. 19* shows one of these projections. It also shows that the fibrils of the developing cone pass into the threads of the surrounding cytoplasmic reticulum, suggesting that they grow at the expense of the cytoplasm. As the cone pushes outward, the meshes elongate proportionately, and the fibrils composing them become much more sharply defined. As in Iris and Disporum, there appears to be no definite number of cones formed; there are usually four or five to be seen in section.

As the apices of the cones approach near to the cell wall, the nuclear membrane breaks down, and the space once occupied by the nuclear sap becomes filled with the ingrowing fibers of the base of the cones (*fig. 20*). By the time the nuclear wall has disappeared, some of the cones unite at their apices. This union continues in the same fashion as that described in Gladiolus, Iris, and Disporum. *Fig. 21* shows a condition in which the nuclear wall has entirely disappeared, and five cones are seen in section. Some of these cones are evidently the result of the union of several primary cones. By the time this stage is reached the fibrils have become long independent threads, converging to the apices of the cones, and many of them have become attached to the chromosomes.

The fusion of the cones is probably a very rapid process, as the multipolar stages were only obtained from material fixed in the field, immediately after being dissected from the plant. They are never found as frequently as the bipolar stage.

Fig. 22 shows the cones uniting into two groups, pointing in opposite directions. Before fusing, the cones point outward in all directions, so that in a section few of them show (*fig. 21*), but as they collect in groups a median section shows many more in the same plane. When the bipolar condition is finally reached, the usual three sets of fibrils are sharply differentiated. The connective fibrils are clearly defined and appear to be thicker in the region of the chromosomes. The continuous fibrils extend uninterruptedly from pole to pole and are much finer than the connective fibrils. Extending laterally from the poles, numerous mantle fibrils are to be seen, with their free ends projecting into the cytoplasm (*fig. 23*).

As shown by the series of figures, the process of spindle development in the first division of Hesperaloe is essentially the same as that described for Gladiolus, Iris, and Disporum. On account of the scarcity of the material, the development of the spindle for the second divisions was not observed.

THE POLLEN MOTHER-CELLS OF HEDERA HELIX.

From the above description, it seems quite evident that there is a very striking resemblance in the method of spindle forma-

tion in Gladiolus, Iris, Disporum, and Hesperaloe. As these types are representative of related families, it is not surprising to find such a resemblance. This method of spindle development, however, is not peculiar to these families, as the following descriptions of the conditions existing in Hedera will show.

The young anthers containing the pollen mother-cells of *Hedera helix* are extremely small and difficult to handle. But after being fixed in the field and imbedded, the difficulties are mostly overcome, for the mother-cells stain very easily with the triple stain, and the various stages in the development of the spindle of the first and second division are readily obtained.

The mother-cells in Hedera are much smaller than the liliaceous plants, but the nuclei are relatively much larger. As division approaches, the amount of nuclear sap is very great, and as a result the nucleus occupies one-half the space of the cell. Before any kinoplasmic differentiation takes place, the cytoplasm presents a uniform granular reticulum, but this appears to be slightly denser in the vicinity of the nuclear membrane, suggesting the condition that exists in Cobaea and Gladiolus. As soon as the chromatin has segmented to form the chromosomes, the cytoplasm in contact with the nuclear membrane becomes differentiated into a thin weft of fibrils, which stain an intense blue. The development of the weft is essentially the same as that described for Gladiolus, Iris, Disporum, and Hesperaloe. It consists at first of only a few threads, which interlace with each other and run more or less parallel to the nuclear membrane. The fibrils nearer the membrane stain a very deep blue, but those farther out stain less, and as they merge into the surrounding orange-staining cytoplasm, they are slightly granular and are no longer to be distinguished from the reticulum of the latter (*fig.* 24). The origin of the fibrils of the weft is apparently due to the change in the structure of the threads of cytoplasm, as described in Iris, Disporum, and Hesperaloe. As in these plants, the weft is uniformly thick in the early stages of its formation, but it soon develops projections at irregular intervals, producing the primary cones of the multipolar figure (*figs.* 25, 26). As the primary cones grow outward, the fibrils composing

them no longer run parallel to the nuclear membrane or interlace with one another. They become long independent fibrils, projecting more at right angles to the nuclear membrane and converging at the apices of the cones. *Figs. 26* and *27* show several of these cones, nearly fully developed.

As the cones approach the completion of their development, the nuclear membrane suddenly disappears, and the fibrils at the base of the cones come in contact with the chromosomes. The fusion of the cones proceeds until there are two groups (*fig. 28*). The chromosomes are very numerous, and the mature spindle is consequently very wide at the equator. The usual connective and continuous fibrils are to be distinguished, but the mantle fibrils do not appear until the chromosomes begin their migration to the poles.

It is quite clear from the series of stages shown in *figs. 24* to *29* that the formation of the first spindle in Hedera is similar to that which occurs in Gladiolus, Iris, Disporum, and Hesperaloe in every essential particular.

In his work on Agave, Osterhout describes two distinct types of spindle formation in the two divisions preceding the development of the pollen. In the second division the spindle originates in a way that is absolutely different from that in the first. There is no weft surrounding the nucleus in the early stages, but instead there is a series of fibrils which radiate out from the nucleus, with their free ends projecting into the cytoplasm. Such a stage as this does not occur in the first division, and it is remarkable that two conditions so essentially different could be found in two succeeding generations of cells. With the idea of ascertaining whether any such difference as this existed in the two succeeding divisions of the mother-cell in Hedera, a very careful examination was made of every stage in formation of the second spindle. This proved quite conclusively that the spindles of the first and second divisions are formed in identically the same fashion.

Very little time elapses between the first and second divisions. As soon as the first spindle reaches the bipolar stage, the chromosomes move to the respective poles and unite, forming

two masses of chromatin at opposite sides of the cell. While this is taking place (*fig. 30*) numerous long mantle fibrils extend from the sides of the masses of chromatin and at the same time the continuous fibrils increase in number. The mantle fibrils, however, are not confined to the lateral position on the chromatin mass, but radiate from all sides of it. These radiating fibrils persist for a considerable time, even after the chromatin has secreted a nuclear sap and surrounded itself with a membrane. *Fig. 31* shows two mature daughter nuclei, with the chromatin in the spirem stage, each surrounded by a distinct membrane. The continuous fibrils between the two nuclei begin to disappear in the equatorial region of the cell, and each nucleus is completely surrounded by a system of radiating fibrils with their free ends projecting into the surrounding cytoplasm. When first observed, the writer mistook this condition for the radiating stage that Osterhout has figured in the formation of the second spindle in Agave. The two conditions are strikingly alike, but a careful study of the stages immediately preceding and following this showed conclusively that the radiating fibrils were the remnants of the first spindle and not the beginning of the second. As shown in the next stage (*fig. 32*), these radiating fibrils and the continuous fibrils disappear completely, and take no part whatever in the formation of the second spindle. As *fig. 32* illustrates, the resting period of the daughter nuclei is a very short one. The chromatin breaks up into chromosomes before the last of the continuous fibrils have vanished.

The first evidence of the beginning of the new spindle is the transformation of the cytoplasmic reticulum close to the daughter nuclei into a weft of fibrils completely surrounding each nucleus (*fig. 33*). In every detail the series of events that leads to the formation of the second spindles is identical with that of the first. Almost every stage in the sequence was carefully examined, and the second was found to be a duplicate of the first series. It will therefore be only necessary to mention the critical stages.

At first the kinoplasmic zone increases uniformly in thickness, and its fibrils run more or less parallel to the nuclear wall.

Very careful search was made for the radial condition described by Osterhout for the second spindle in Agave, but nothing like this was found. The fibrils are never radial at this stage.

Having reached a certain thickness the weft no longer increases uniformly, but grows out at irregular intervals from the primary cones of the spindle in identically the same fashion as it does in the formation of the first spindle (*fig. 24*).

SUMMARY.

1. In Iris the formation of the spindle is initiated by the transformation of the cytoplasmic reticulum close to the nuclear membrane into a weft of kinoplasmic fibrils, which forms a complete zone about the nucleus.

After increasing to a certain thickness, the zone projects outwards at irregular intervals, forming a series of cones which terminate in sharp points.

The cones apparently develop at the expense of the cytoplasmic reticulum into which they project, and as they grow the fibrils composing them lengthen and converge at the apex.

During the complete formation of the primary cones the nuclear wall persists.

Upon the breaking down of the nuclear membrane the cones fuse until there are two groups of them pointing in opposite directions.

The points at which the cones forming these groups meet at their apices become the poles of the bipolar spindle.

2. In Disporum the first indication of the spindle is the formation of a weft of kinoplasmic fibrils which partially surrounds the nucleus. As in Iris, the fibrils composing the weft are formed by the transformation of the cytoplasmic reticulum. Unlike Iris, the meshes of the weft do not run parallel to the nuclear membrane.

The weft increases irregularly, forming several projections which become the primary cones of the spindle. As they grow outward the cones become sharp-pointed and their fibrils are sharply defined. It is very clear that the kinoplasmic weft is of cytoplasmic origin.

After the cones have developed the nuclear wall breaks down, and the cones unite in two groups to form the bipolar spindle.

3. As in Iris and Disporum, the spindle in Hesperaloe originates from a weft of kinoplasm. The latter completely surrounds the nucleus and is of cytoplasmic origin. As in Iris, the fibrils of the weft run parallel to the nuclear membrane.

By growing out at irregular intervals the weft develops a series of sharp-pointed projections which become the primary cones of the spindle.

As the nuclear wall disappears, the cones collect in two groups and fusion at their apices brings about the bipolar condition.

4. In Hedera, as division approaches, the cytoplasm close to the nucleus becomes changed into a weft of kinoplasmic fibrils, which orms a zone completely surrounding the nuclear membrane.

This change in the form of the cytoplasm proceeds at intervals in such a way that the kinoplasmic zone appears to grow out in the form of projections. These projections terminate in sharp points and become the primary cones of the spindle.

As the cones grow outward the fibrils composing them become more sharply defined, elongate, and converge at their apices.

The events that follow are essentially the same as those in Iris, Disporum, and Hesperaloe.

The method of spindle formation of the second division is a duplicate of the first.

5. While the various methods of spindle formation described for the higher plants differ in certain respects, the resemblances between others are sufficiently great in warranting a classification of them. The following classification of the types is therefore suggested:

Type 1, represented by Gladiolus, Iris, Disporum, Hesperaloe, Hedera, Osmunda.

Type 2, represented by Cobaea, Passiflora, Lavatera.

Type 3, represented by Equisetum.

Type 4, represented by Agave.

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EXPLANATION OF PLATES XV AND XVI.

The figures were drawn with the Abbé camera, Zeiss apochromatic immersion obj. 12^{mm}, 1.30 ap., compensating ocular no. 6.

PLATE XV.—FIGS. 1–11. *Iris florentina.*

FIG. 1. A pollen mother-cell; cytoplasm in contact with nuclear membrane transformed into a weft of kinoplasmic fibrils, forming a narrow zone surrounding nucleus.

FIG. 2. Slightly older stage; kinoplasmic weft of considerable but not uniform thickness, preparatory to forming primary cones of spindle.

FIG. 3. Older; outward projections of the weft developed into a distinct sharp-pointed cone. Fibrils composing the cone no longer parallel to the nuclear wall, but directed outward and convergent at apex of cone.

FIG. 4. Like *fig. 3*, but also shows that cones do not develop simultaneously.

FIG. 5. Two cones nearly fully developed; a third beginning.

FIG. 6. Three primary cones of about the same size. Up to this stage nuclear wall is intact, taking no part in formation of kinoplasmic weft; nucleolus also persistent and now vacuolate.

FIG. 7. Nuclear wall and nucleolus have partly disappeared; fibrils at base of cones have grown inward and some have joined chromosomes.

FIG. 8. A characteristic multipolar figure; the three cones have evidently resulted from the union of several primary cones.

FIG. 9. Somewhat older stage showing further fusion of cones at their apices.

FIG. 10. Cones have united into two groups with their apices pointing in opposite directions, indicating the position of the bipolar spindle.

FIG. 11. Mature spindle.

PLATE XV.—FIGS. 12–17. *Disporum Hookeri.*

FIG. 12. Spore mother-cell showing transformation of cytoplasm into a weft of kinoplasmic fibrils not parallel to the nuclear wall.

FIG. 13. Later development of kinoplasmic zone; the weft not uniform but much more abundant on one side of nucleus.

FIG. 14. Weft in the form of irregular sharp-pointed primary cones; their fibrils very much elongated and convergent.

FIG. 15. Fibrils forming cones more independent of one another and more sharply defined.

FIG. 16. Nuclear membrane gone; cones united at apices; fibrils joined with chromosomes; the latter taking position at the equator.

FIG. 17. Mature bipolar spindle.

PLATE XVI.—FIGS. 18–23. *Hesperaloe Davyi*

FIG. 18. Pollen mother-cell, showing formation of kinoplasmic zone quite uniform in thickness.

FIG. 19. Later irregular outward growth of kinoplasmic zone; the meshes composing it point in the direction of the outward projection or primary cone.

FIG. 20. Nuclear wall breaking down; inward growth of fibrils from the base of the cones with which the chromosomes are now in contact.

FIG. 21. Typical multipolar spindle after entire disappearance of nuclear membrane.

FIG. 22. Cones collecting in two groups and uniting at their apices so as to indicate position of bipolar spindle.

FIG. 23. Mature bipolar spindle.

PLATE XVII.—FIGS. 24–34. *Hedera helix*

FIG. 24. Young pollen mother-cell showing early stage in the formation of kinoplasmic weft.

FIG. 25. Later stage of kinoplasmic zone, indicating by one-sided growth the beginning of one of the primary cones.

FIG. 26. Four more fully developed primary cones in the same plane; fibrils composing them much more clearly defined and convergent.

FIG. 27. Somewhat older stage with several cones in the same plane; fibrils very clearly defined and cones almost fully developed.

FIG. 28. Nuclear wall gone; chromosomes in contact with spindle fibrils; cones partially united in two groups indicating future position of bipolar spindle.

FIG. 29. Mature bipolar spindle. As there is a large number of chromosomes, the spindle is very wide at the equator.

FIG. 30. Chromosomes at the poles of spindle; nuclear wall not yet formed around daughter nuclei; many continuous fibrils between the daughter nuclei; also a series of short radiating mantle fibrils, which extend out in all directions from the masses of chromatin.

FIG. 31. Daughter nuclei with membranes; chromatin in spirem condition; continuous fibrils disappearing midway between the daughter nuclei; system of radiating fibrils persistent.

FIG. 32. All fibrils of first spindle have disappeared; chromosomes of daughter nuclei ready for second division.

FIG. 33. New weft of kinoplasmic fibrils forming a zone about each daughter nucleus, the first indication of spindles for second division.

FIG. 34. Weft growing out from one of the daughter nuclei to form primary cones of second spindle.

THE EMBRYO SAC OF CASUARINA STRICTA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. L.

THEODORE C. FRYE.

(WITH PLATE XVII)

IN the examination of the embryo sac of Asclepias (2) the writer was impressed with the long resting period of the egg between its fertilization and its first division. The difficulty of distinguishing a fertilized from an unfertilized egg suggested that in some cases in which fertilization was reported to take place after the division of the endosperm nucleus, an error had crept in, an unfertilized egg being mistaken for a fertilized one. If there is fertilization after endosperm division, the fate of the second male nucleus is an equally interesting question. This suggested a reinvestigation of the sac of Casuarina, the results of which are here presented.

The admirable paper of Treub (5) on Casuarina appeared in 1891. In a review of it by Chamberlain (1) in 1896, five years after it was published, the following suggestive statement is made:

> I have been deeply interested in Casuarina's embryo sac without antipodals, as I have been studying Salix and for more than a year was unable to discover any trace of antipodals. However, Salix has antipodals, as some of my preparations now prove. Some slides also show the fushion of polar nuclei to form the endosperm nucleus. There is no doubt that the antipodals of Salix are very transitory, but they are formed nevertheless. It may be that Casuarina has antipodals of this evanescent character. Since the technique betrayed by Treub's figures and text could be greatly improved, I should be glad to see the Casuarina sac studied again in much greater detail, in order that Treub's conclusion may receive additional confirmation or be corrected.

A résumé of the more essential features of Treub's paper is as follows: The species studied were *C. suberosa*, *C. Rumphiana*, and *C. glauca*. The pistillate flowers are naked, occurring in the axils of small bracts that form a cone-like cluster. Each pistil consists of two carpels whose inner surfaces soon fuse along

their lower part. Lateral placental outgrowths divide the ovarian cavity into two loculi, but from this central placenta two ovules usually arise, both of which, except in rare cases, form in the same loculus. The funiculi are curved downward so that the ovules lie with the chalaza in the base of the loculus and the micropyle toward the style. Several hypodermal cells ("primary mother-cells"), possibly archesporial in nature, become deeply situated on account of their own transverse divisions and form a multicellular sporogenous tissue, sharply differentiated laterally, as in pteridophytes. Later it is also well differentiated toward the micropyle, but not in the region of the chalaza, where a strong "intercalary growth" takes place, suggesting the origin of sporogenous tissue from cells not arising from the primary sporogenous cells. Of the sporogenous cells,[1] some function as spore mother-cells, some remain small and are soon resorbed, while in some species others become tracheids, recalling the formation of elaters among the liverworts. Those that function as spore mother-cells divide, each forming a row of four. Thus with pteridophytic sporogenous tissue, there is spermatophytic arrangement of megaspores. Some of these enlarge, forming embryo sacs, as many as a score of sacs being counted in a single ovule. They elongate more or less antipodally, some even penetrating the chalaza to the funiculus. Differing from almost all other spermatophytes, the functionless megaspores of Casuarina are not resorbed, but remain among the fully developed embryo sacs. Whatever the number of ovules in an ovary, only one is fertilized. The sacs in the unfertilized ovules enlarge, become binucleate, but form no antipodal prolongations. In the fertilized ovules not all the megaspores that enlarge form prolongations; those not centrally placed are often arrested early. In the fertile ovule only one sac is fertilized.

The formation of cells within the sac was not definitely traced,[2] but developing sacs with one nucleus, and sometimes with two nuclei, were found. A certain nucleus, of unstated

[1] Treub applies the term "sporogenous" cells to the tissue both before and after the formation of megaspores.

[2] It will be remembered that this work was done twelve years ago.

origin, near the micropylar end, is itself the egg, or develops the sex apparatus of one to four cells, usually three, one of which is the egg. The others (synergids), it is thought, are homologous with the neck cells of gymnosperms and pteridophytes. Treub draws this conclusion from their origin from a single micropylar cell with cellulose wall, and from their appearance. There are no antipodals.

This was the first case of chalazogamy reported. The passage through the chalaza is facilitated by the presence of the prolongations of the sterile megaspores, into which the tube enters, leaving them to reach the egg apparatus that is to be fertilized. It is stated, however, that the tube never enters the fertilized sac, but becomes attached to it at some point between the egg apparatus and the antipodal region. Sometimes a nucleus was observed in the tube, but never more than one.

The egg remained unchanged for some time before its fertilization. The exact moment of fertilization was not determined, but before it occurred the formation of a large number of endosperm nuclei had taken place, even as many as fifty. This conclusion was based on the fact that sacs were found which formed endosperm before the pollen tubes reached them.

Casuarina thus shows a megasporic sporogenous tissue reminding one of the pteridophytes, a number of embryo sacs suggesting gymnosperms, and "synergids" suggesting the canal cells of gymnosperms; and it was unique in the route of the pollen tube. These considerations led Treub to believe that the Casuarinaceae are intermediate between angiosperms and gymnosperms.

The species that I studied was *Casuarina stricta* Ait. The material was collected in California from introduced trees by Mr. Albert C. Herre and identified by him. It was killed in chrom-acetic acid; but unfortunately the pieces were large, and hence the killing was not rapid enough to catch cells in mitosis. Only the pistillate cones were secured. The ovaries were carefully teased out with needles and sectioned in paraffin. Longitudinal sections $5\,\mu$ thick and stained with safranin and gentian-violet were found to be the most satisfactory. The work was almost all done at night. Light was obtained from a gas-lamp

provided with a Welsbach mantle, and passed through an eight-inch globe filled with a half-saturated aqueous solution of copper sulfate. In this connection I wish to acknowledge my obligation to Mr. Alexander G. Ruthven and Miss Myrtilla M. Cook for assistance in the preparation of slides, etc.

The young cones, about 5^{mm} long, are covered with what appear to be hairs, but upon examination these prove to be the ends of the filiform carpels. The ovaries are flattened laterally, in contrast to the adaxial flattening of the wings in Pinus. The carpels show numerous crystals in a stratum of cells near their inner surfaces, a condition quite similar to that figured by Treub in *Casuarina suberosa*. The origin of the placenta was not traced, but the ovules arise laterally from a central placenta near its base, as Treub has reported in other species.

The two integuments arise normally (*figs. 1, 2, 18*) and leave a micropylar opening to the nucellus. About the time of their origin one would expect to find the archesporium. In the hypodermal layer at this stage there are certain cells (*fig. 3, a*) which may be interpreted as archesporial, but such an interpretation rests alone upon the form and size, and the relation of cells in that vicinity to each other later; the usual stains would not differentiate the cells either by darker stain or by showing larger nuclei. From *fig. 4* it seems that the archesporial cells divide by walls parallel to the surface. Possibly this is the division into primary wall and primary sporogenous cells, but there is only the evidence of other plants, which is insufficient. Mitosis in the succeeding divisions of cells *b*, *fig. 4*, showing presence or absence of reduction in chromosomes, would settle it, but no spindles were found. However, by further division of cells *a* or *b* or both, in *fig. 4*, a stage like *fig. 5* is reached. More transverse walls and greater elongation result in rows of cells being formed (*fig. 6*), of which the outer ones form the wall tissue and the inner ones the sporogenous tissue. The general arrangement of cells in rows, and the relative position of sporogenous tissue with regard to sterile tissue in comparison with the same in other spermatophytes, especially in the anthers, and in Selaginella, lead me to surmise that cells *a* and *b* of *fig. 4* give

rise, respectively, to wall tissue and sporogenous tissue. The occurrence of massive sporogenous tissue, as reported by Treub, is an indubitable fact. Its limits are well defined laterally by the larger cells and larger nuclei of the sporogenous tissue. At the ends it grades more or less into the surrounding parenchyma, and the cells near the microple appear younger than those toward the chalaza. I am inclined to believe that the nucellus as it elongates carries with it the primary sporogenous cells, each of which leaves behind by its own division a train of sporogenous cells. The formation of sporogenous tissue near the chalaza from other than sporogenous cells, as suggested by Treub, was not observed, and is believed not to occur in *C. stricta*. According to Treub, some of the sporogenous cells absorb others, but nothing of the kind was found in *C. stricta*. Either this species differs from those studied by him, or the absorption of sporogenous cells has been confounded with the absorption of megaspores. *C. stricta* forms no tracheids in the sporogenous tissue, agreeing in this with Treub's report for *C. suberosa*. The cells of the sporogenous tissue are several times as long as wide (*fig. 6*), while later, when the embryo sacs begin to form, only approximately isodiametric cells are apparent. This makes me believe that Treub was right in his statement that the formation of four megaspores occurs here. A further reason for my conclusion, and a stronger one, is that later groups of four in a row are recognizable (*figs. 8, 9, 10*).

The differentiation of megaspores begins quite soon after their formation. Usually one of each group of four starts, but sometimes more (*figs. 10, 14*). Many get no further than an enlarged nucleus, while others reach various stages of development, up to an apparently fertilizable sac. A row of four, as in *fig. 10*, certainly presents a strong argument, if any further argument is required, for the megasporic nature of the cells composing such a row in angiosperms. The sterile megaspores are not all resorbed; but some certainly are, and it seems to me that most of them are. The number of sacs reaching maturity varies greatly in different ovules, but ranges from two to twelve. These are mostly those of central location, forming an axial core in the megasporic tissue.

The embryo sac passes through the normal 1, 2, 4, and 8-celled stages (*figs. 9, 10, 14, 15*). These stages were not all seen in sacs which eventually become fertilized, for among so many sacs which reach maturity one cannot tell which will be the favored one until it is approached by the pollen tube. However, if one finds all these stages in embryo sacs arrested in various degrees of development, one may with reason conclude that the one later fertilized passed through the same stages, especially since some which remain sterile reach a development equal to that of the one later fertilized, so far as could be determined. As many as twelve, each having a fully developed egg apparatus, were found in a single ovule.

Within well-developed sacs three cells are organized at the micropylar end, forming the egg apparatus (*figs. 14, 16, 17*). In *fig. 14, C*, the cells have not yet collected definitely enough to make it certain which will form the egg apparatus. It is surmised, however, that three of the cells *a*—*d* will function as such; *e* is probably the antipodal polar. From *figs. 10, 14, 15, 16*, I can see no escape from the conclusion that the egg apparatus is normal in its origin. These figures are not exceptions chosen here and there to prove a point. They can easily be duplicated. *Fig. 16* is indeed the type of a fully developed sac in this species. An examination of the egg apparatus in *figs. 15, 16, 17* shows that there is considerable variation in the form of the cells composing it in the different sacs. The egg itself cannot be distinguished from the synergids in most cases. Sometimes cases occur showing less than three cells in the egg apparatus, but these are few in number, and it seems to me do not warrant a conclusion that Casuarina is different in this respect from other angiosperms.

Normally there are three antipodals. Comparing *figs. 10* and *14*, the latter is evidently the older group of megaspores. What is seen in *fig. 14, C*, is just what would be expected in the development of a normal sac. Of the eight cells in *fig. 14, C*, three (*f*) are collected in a depression in the antipodal region, just as one might expect, and about them is massed a quantity of protoplasm almost, if not completely, separated from the rest

of the protoplasm of the sac, strongly suggesting the separation of these cells by a wall. Comparing now *fig. 14, C*, with *fig. 15*, a slightly older sac, the antipodals in the latter certainly cannot be questioned. The whole sac is typical enough of angiosperms to serve as a conventional prefertilization sac. However, as has been remarked, *fig. 16* is more typical of the sac of *C. stricta*. In the older sacs (*figs. 16, 17, 20*) these antipodals resemble the unabsorbed megaspores very much, and could easily be mistaken for them. This might account for their reported absence, unless other species differ in this respect from *C. stricta*.

Sometimes, however, no antipodals were found (*fig. 21*), and the reason for this may be considered. Some of the sacs develop long antipodal prolongations (*figs. 14, 17, 20*), and these do not always appear at the same time. *Fig. 11, a* shows one already under way when the sac is in the 2-celled stage, and 4-celled stages were also found showing the beginning of antipodal prolongations. *Fig. 13* may be developing one at *a*, although that cannot be said with certainty. In a case like *fig. 11*, when the sac reaches the 8-celled stage and the antipodals settle at some point, where will they likely be found? If they seek the antipodal end, they will likely slip into the antipodal prolongation and perhaps be found somewhere within that. At least such a thing seems quite possible. The antipodal prolongations, however, are long tortuous tubes, very much entangled with their fellows. It is almost impossible to trace a definite one to its end with certainty. Much more is it difficult to determine the number of nuclei within, when above and below it are scattered unresorbed undeveloped megaspores. There are nuclei within these prolongations in some cases in which antipodals are wanting, but I was not certain of the number in any case. However, in one case there were three cells (*fig. 14, D, h, i, j*) at various distances down the tube. If in this sac the polars had already united, all the nuclei are accounted for. Sometimes, however, the antipodal prolongations are not formed until late in the history of the sac (*figs. 14 C, 15*). If it occurs after the antipodals have become inclosed by walls and perhaps adhere to the walls of the sac (*fig. 16, a*), their presence in the body of the sac,

notwithstanding the presence of an antipodal prolongation, is explained. Thus I believe we have the solution of the antipodal problem in Casuarina. Some of the antipodal prolongations grow so long that they penetrate the chalaza, occasionally passing slightly beyond it into the funiculus.

The location of the polar nuclei is quite various. Like the antipodals, they seem occasionally to pass into the antipodal prolongations (*figs. 14 D, 17*), and are lost in the maze of tubes. Sometimes only one was found (*fig. 16, e*), but in this case the polars may have fused and this is the endosperm nucleus. The sac then, except for the antipodal prolongation and its consequent effect upon the location of the antipodals and the endosperm nucleus, seems to be normal in its development.

Only one pollen tube penetrates a flower, hence only one ovule is entered and only one embryo sac in that ovule is fertilized. The favored sac was in all the observed cases near the micropylar end of the megaspore group. The pollen tube enters the ovule as Treub has stated (5). Coming down the central placenta (*fig. 18*), it wanders somewhat in the region where the funiculus has its origin, as though the attractive influence, or whatever it is that guides it, were not sufficiently strong to guide it with certainty. The tubes again frequently branch just before entering the chalaza (*fig. 18, b*). Sometimes the branches reach the surface, as Treub says, and he suggests two possible reasons for the branching: (*a*) for aeration; this is suggested by their often reaching the surface; (*b*) for holdfasts to anchor the tube firmly before it makes its entry into the nucellus. Neither of these appeals to me very strongly, and for the latter I see no reason at all. The cause is probably the same as that which causes wandering at the point of entry into the funiculus.

The tube seems to enter the prolongation of one of the embryo sacs and thus finds an easy passage through the chalaza. The plugs of cellulose in the tubes at intervals, as reported by Treub, are quite rare in *C. stricta*, and when present are short, resembling more a thick transverse wall than a plug. In the maze of tubular antipodal prolongations I was not able to follow the pollen tubes with certainty, and cannot therefore say whether

the end is separated from the main body, as Treub claims, or not. When it approaches the sac that it ultimately fertilizes, it is sometimes free (*fig. 20*), and sometimes apparently within the prolongation of the very sac whose egg apparatus it is destined to reach (*fig. 21*). I doubt whether there is any fixed path within the nucellus for the tube. It probably follows the path of least resistance so long as it leads in the direction whence comes the guiding stimulus, whatever that may be.

The sperms were observed near the chalaza in several preparations, as small rounded nuclei accompanied by the tube nucleus (*figs. 18, 19*). They were again seen, still spherical, in the tube near the sac about to be fertilized (*fig. 21*), and here too the tube nucleus was close behind them. This nucleus is easily distinguished from the sperms by its comparatively large size. In *fig. 20* the sac, which is evidently quite near the point of fertilization, shows only two antipodals, and there is one nucleus missing in the egg apparatus. The nuclei *p* are probably the two polars. It would be possible to regard these as two endosperm nuclei, but no reason for doing so appears.

Fig. 21 is a case of "double fertilization." In this the tube, or its contents, apparently entered by way of the antipodal prolongation. The sperms are crescentic bodies, one slightly larger than the other. The two polar nuclei have not yet united. I see no reason for any other interpretation of the two polars; if they are endosperm nuclei, we have a unique case in the fusion of a sperm with endosperm. Which of the three micropylar nuclei is the egg I cannot say, but it is probably the one containing the larger spherical nucleus, or that containing the elongated nucleus. No antipodals are in evidence, but they are probably in the antipodal prolongation. The sperms evidently elongate within the sac or very near it, as in Asclepias (2).

I am convinced that no such endosperm formation before fertilization occurs as Treub thought, and my reasons are as follows:

1. The cases of fertilization observed (*figs. 20, 21*) show no endosperm.

2. The pollen tube sometimes enters the ovule before the embryo sacs are ready for fertilization. In one case pollen

tubes were found in the funiculus before the division that results in the four megaspores, and at various times tubes had passed the chalaza while there was no sign of endosperm in the sacs. Usually when a tube gets close to the sac its penetration is rapid, and Treub says its growth within the nucellus is rapid. It seems, then, that there would not be time for a great development of endosperm between the time of the entry of the tube into the chalaza and its entry into the sac.

3. Inferring the exact time of fertilization from the presence of pollen tubes is not conclusive. Anyone who has tried to distinguish a pollen tube in the confused strand of tubular antipodal prolongations will readily understand the difficulty of determining without a doubt what is tube and what is sac. Even if tubes are seen, it is not an easy matter to tell whether they are young or old, and it must have been much more difficult with teased preparations.

4. Very little was said or known twelve years ago about the retarded division of the egg. Now it is known that the angiosperm egg often rests for a time after its fertilization, while the formation of endosperm begins at once. It was the writer's good fortune to study such a phenomenon in the embryo sac of Asclepias (2), in which the exact time of fertilization was observed, and the egg rested after fertilization until the endosperm had passed its 16-celled stage. If the exact time of fertilization had not been seen, one would have been apt to judge the resting fertilized egg to be an unfertilized one, and would have been inclined to say that endosperm division took place before fertilization. Johnson's study of the Piperaceae (3) has brought to light the same resting period in the egg of *Piper medium*. He figures a sac with twenty-two endosperm nuclei in cross-section, already walled off, and the egg still undivided. In the same paper he says of *Heckeria umbellata* that the embryo sac becomes filled with cellular endosperm before the egg divides. It is only fair to add, however, that fertilization was not observed in these species, but the appearance of the egg leaves little doubt of its fertilization long before it divides.

5. The fact that Treub found a definite wall about the egg in

most cases suggests a post-fertilization stage. The rounded form of his figures of eggs also suggests the same.

Unfortunately, the material at hand showed no embryos nor endosperm, the oldest showing that the pollen tubes had reached the sac. It would have been quite interesting to note the condition of the egg during endosperm development. But if one supposes that Treub mistook a fertilized egg for an unfertilized one—a thing which might even be possible with the technique of today, to say nothing of twelve years ago—and if he further mistook a discharged pollen tube for an undischarged one, the formation of endosperm before fertilization would be eliminated from his own account. It will be recalled here that he himself could not be certain about seeing nuclei in the pollen tube except in a few cases, and in no case is more than one suggested. From the size of the tube nucleus (*fig. 20, t*) one is led to conclude that he saw it rather than a sperm.

A summary of my results with *C. stricta*, as compared with Treub's with *C. Rumphiana*, *C. glauca*, and *C. suberosa*, may be stated as follows:

There is agreement as to the bilocular ovary, the presence of two ovules in an ovary and both in the same loculus, the presence of two integuments and a micropyle, the upright ovules that arise laterally from the central placenta, the multicellular archesporium consisting of a hypodermal plate of cells, the massive sporogenous tissue, the division of each spore mother-cell to form four megaspores, the numerous mature sacs in an ovule, the long antipodal prolongations of the sacs, the fertilization of only one embryo sac in every ovary, and chalazogamy.

There is disagreement as to the origin of the sporogenous tissue, in *C. stricta* all of it arising from the hypodermal archesporial plate, while Treub believes that some sporogenous tissue near the chalaza does not arise from this plate; as to the resorption of sporogenous cells, which Treub claims, but I was not able to observe; as to the sequence in the formation of the embryo-sac structures, which differs in no way in *C. stricta* from the sequence usual among angiosperms; as to the character of the egg-apparatus, which differs in no way in *C. stricta* from that

of other angiosperms; as to the presence of antipodals, which are certainly present and normal in number in *C. stricta;* as to the relation of endosperm formation to the time of fertilization, Treub reporting much endosperm before fertilization, and in *C. stricta* fertilization clearly taking place before endosperm-formation.

The additional facts, not observed by Treub, are the occurrence of "double fertilization," and the presence of two sperms, spherical in the pollen tube and crescentic in the sac.

My thanks are due to Professor John M. Coulter and Dr. Charles J. Chamberlain for valuable assistance in the prosecution of the work and in the publication of the results.

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EXPLANATION OF PLATE XVII.

All drawings were made with a Bausch & Lomb camera lucida, $\frac{2}{3}$, $\frac{1}{6}$, $\frac{1}{12}$ (oil) objectives, and nos. 1 and 2 oculars. The figures have been reduced one half, but the original magnifications are given.

Casuarina stricta Ait.

FIG. 1. Young ovule: *n*, nucellus; *i*, inner integument; *l*, loculus without ovule. × 207.

FIG. 2. Ovule: *n*, nucellus; *o*, outer integument; *i*, inner integument. × 140.

FIG. 3. Nucellus about same stage as in *fig. 2; a*, cells which may be archesporium. × 1366.

FIG. 4. Nucellus with hypodermal periclinal wall-formation, suggesting that *a* may be primary wall cells, and *b* primary sporogenous cells. × 1366.

FIG. 5. Nucellus, suggesting that interior cells *r* arise from hypodermal cells at apex. × 1366.

FIG. 6. Nucellus: *s*, massive sporogenous tissue within, with well defined lateral limits. × 900.

FIG. 7. Spore mother-cell about to divide, showing chromatin threads; the cells are longer, the section is diagonal. × 1950.

FIG. 8. Row of four megaspores; *m*, micropylar end. × 1950.

FIG. 9. Row of four megaspores, the middle ones enlarging; *m*, micropylar end. × 1950.

FIG. 10. Row of four megaspores in various stages of embryo sac formation; *m*, micropylar end. × 1950.

FIG. 11. Two-celled embryo sac; antipodal prolongation (*a*) already begun. × 1950.

FIG. 12. Two-celled embryo sac; *m*, micropylar end; no well defined antipodal prolongation. × 1950.

FIG. 13. Four-celled embryo sac; *a*, possibly beginning of antipodal projection. × 1950.

FIG. 14. Row of four megaspores derived from one spore mother-cell and older than those in *fig. 10*; *m*, micropylar end; *A*, arrested megaspore; *B*, megaspore probably arrested after some internal cell division, but now disintegrating; *C*, 8-celled sac; *a, b, c, d*, will probably form egg apparatus and micropylar polar; *e*, probably antipodal polar; *f*, antipodals with suggestion of wall formation; *D*, 7 or 8-celled sac with antipodal prolongation: *h, i, j*, probably antipodal and polar or endosperm cells. × 1950.

FIG. 15. Eight-celled embryo sac; *a*, antipodal; *p*, point where antipodal projection may be expected to arise; *po*, polar nuclei. × 1950.

FIG. 16. Typical embryo sac without the long antipodal prolongation; *e*, endosperm nucleus; *a*, antipodals. × 1950.

FIG. 17. Embryo sac with more elongated cells in egg apparatus; only two antipodals found; *a*, polar nuclei or one endosperm and the other antipodal. × 1950.

FIG. 18. Pollen tube approaching the nucellus; *b*, branch of tube; dotted line bounds sporogenous tissue. × 140.

FIG. 19. Part of *fig. 18* enlarged; *t*, tube nucleus, *s*, sperms. × 1366.

FIG. 20. Pollen tube just having reached the embryo sac; *pt*, pollen tube; *t*, tube nucleus; *s*, sperms; *a*, antipodals; *p*, polars, one nucleus in egg apparatus and one antipodal missing. × 1950.

FIG. 21. A case of double fertilization; *s*, sperms; antipodals not found in this preparation. × 1950.

ON THE GAMETOPHYTES AND EMBRYO OF TAXODIUM.

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY, No. 1.

W. C. Coker.

(WITH PLATES I–XI)

(*Concluded from p. 27*)

FORMATION OF VENTRAL CANAL NUCLEUS.

Murrill ('00) has recently described in Tsuga a peculiar method of spindle-formation in the division of the central cell of the archegonium. He finds a kinoplasmic area in contact with the inner side of the nucleus just before its division. Fibers begin to grow from this area into the nucleus, pressing before them the nuclear wall. They gradually extend until they come to occupy the greater part of the nuclear cavity, and are then joined by similar fibers which have come in from the opposite pole to form the prophase of the spindle. These observations I cannot confirm in Taxodium. *Figs. 76–90* show this division in detail. As already stated, fibers pass around the nucleus from the kinoplasmic areas or aster and merge insensibly into the nuclear wall. The nuclear wall is frequently considerably drawn in at a point opposite the kinoplasmic body (*figs. 76, 78*), but no strong fibers can be seen extending from one to the other at this point. In fact, this collapse is generally more noticeable in the early stages of preparatory changes. Murrill ('01) finds such fibers, which he concludes have caused the depression of the nuclear wall.

The arrangement between aster and nucleus at this time may be best compared to that between the car of a balloon and the bag above it, the ensheathing fibers of the nucleus terminating in the aster representing the ropes around the balloon connecting it with the car below. *Fig. 76* shows the beginning of the changes in the nucleus which lead to the formation of the spindle.

Synapsis has occurred, and the nuclear reticulum forms a dense tangle near the nucleolus. The latter can now be distinctly seen to be of compound structure, and from it threads can be traced into the network. Fine threads also connect the conspicuous central tangle with the nuclear walls. Such a synapsis stage is described by Murrill in the nucleus of the central cell of Tsuga. In *fig. 72* the reticulum has begun to move back into its original position. The nucleolus is now distinctly fragmented into a number of granules of apparently equal size, which gradually become more and more separated into a broken ring or coiled thread (*figs. 78–80*). These granules retain the deep red stain characteristic of the nucleolus in previous stages. The ring, or thread, is now broken up more and more into separate parts and distributed near the periphery of the nucleus (*figs. 81–84*) and the reticulum of the nucleus begins to arrange itself for the formation of the spindle (*figs. 83–85*). The fibrous connections between the reticulum and the nucleolar thread are to be noticed at all stages of its distribution.

The red-staining granules derived from the nucleolus have not lost their identity at any stage. They become gradually elongated and thin (*figs. 85, 86*), and thus approach more and more the characteristic structure of the chromosomes. The fibers of the reticulum draw together at different points of the nucleus and certain centrally placed ones become distinguishable as spindle fibers, while the mantle threads pass gradually into the unmodified reticulum of the nucleus. The granular nature of the spindle is evident even at so late a stage as *fig. 86*. The nuclear wall has meanwhile disappeared, but its position is indicated by the arrangement of the fibers until the anaphase stage of division (*fig. 87*). The chromosomes, as they are drawn apart, are of the usual V or U shape (*fig. 87*). The transformation of the nucleolus into the chromosomes may be followed without interruption through its whole course, not only by reactions in staining, but in serial development.

Chromatin nucleoli have frequently been described, but principally among the lower plants. Strasburger ('00) in his recent work devotes considerable space to the discussion of the part

played by the nucleolus in the formation of the spindle. He reviews the present knowledge of the subject, and while acknowledging the chromatin character of the nucleolus in a few cases, expresses himself as strongly inclined toward the view that in the higher plants at least it is of kinoplasmic or spindle-building material. Nucleoli of chromatin character have been described in Corallina by Davis ('98), in Spirogyra by Mitzkewitsch ('85), in Bignonia by Duggar ('99), and in a number of other plants. That the nucleolus of the central cell in Taxodium is directly transformed into chromosomes seems to be evident from the figures given, and I think we may be equally sure of the intranuclear origin of the spindle. The kinoplasmic mass at the tip of the spindle seems to serve merely as a point of attachment for the spindle fibers, its numerous radiations making a firm foundation for the orientation of the spindle, as suggested by Murrill ('01).

The nucleus of the central cell, just before its division, is generally situated not far from the tip of the archegonium, but it is often found as much as a third of the way down. In such cases the central vacuole, which is now much smaller, lies nearer the base of the archegonium. The wall of the nucleus is at the very surface of the cell (*figs. 66, 78*), and it is often impossible to distinguish any protoplasm between nucleus and surface. In *figs. 88* and *89* there is to be noticed in the center of the spindle a broad zone which is composed of numerous granules. In Flemming's triple this zone stains a deeper violet than the other parts of the spindle, and occupies the position at which we might expect to find a cell plate. No cell plate is formed, however, and the whole spindle fades away into the cytoplasm of the cell. At the surface end of the spindle shown in *fig. 87* a small aster has appeared. The daughter nuclei are formed in the centers of these asters (*fig. 88*), and as they increase in size the kinoplasm is collected more and more on the sides toward the spindle (*figs. 89, 90*). In this way the egg and ventral canal nuclei are both furnished with a tuft of kinoplasm on their inner faces. Other tufts may be located at different positions around the egg nucleus (*fig. 90*), but in

later stages the egg nucleus is nearly always furnished with but a single tuft on the side toward the base of the archegonium. The spindle may be situated in every position in reference to the axis of the archegonium, parallel (*fig. 87*), perpendicular (*fig. 88*), or inclined (*figs. 86, 89*), but the inner pole is always located in the center of the aster. The spindle may extend either up or down from the inner pole, and the ventral canal nucleus may thus be placed either above or below the egg nucleus (*fig. 91*). The archegonium to the right in *fig. 92* shows a ventral canal nucleus situated nearer the base than the tip, and in the archegonium to the left the ventral canal nucleus occupies a nearly central position, the egg nucleus lying even lower. It is only rarely that the ventral canal nucleus is situated at the very tip of the egg. Such a position is shown in *figs. 87* and *90*.

This formation of the ventral canal nucleus in any region other than near the tip of the archegonium has not been described in any other gymnosperm so far as I am aware. This peculiarity in Taxodium seems to be an acquired character for the protection of the ventral canal nucleus during fertilization, for, as we are to see later, it is to play a part in the subsequent history of the egg. In most gymnosperms the ventral canal nucleus is furnished with a certain amount of protoplasm of its own which is distinctly separate from that of the egg. Arnoldi ('00) lays stress on what he calls the absence of a ventral canal cell in Cephalotaxus. He considers the ventral canal cell lacking because no wall is formed between the ventral canal nucleus and the egg. In this case, however, a certain amount of protoplasm becomes disorganized around the ventral canal nucleus, and swelling up is said to burst open the neck of the archegonium. If this is the case, the disorganizing protoplasm may be considered as belonging to the ventral canal nucleus, and a ventral canal cell could not strictly be said to be absent.

In Taxodium, however, not even a cell plate is formed, and the ventral canal nucleus lies perfectly free in the cytoplasm of the egg without a distinct protoplasmic area of its own. A ventral canal cell in the strict sense is therefore lacking here.

From Strasburger's ('79) account it seems probable that this is equally true in the Cupresseae. Ikeno ('01) has well remarked that the important point is the division of the nucleus and not the separation of a small amount of protoplasm from the egg. Arnold ('99) denies the occurrence of even a ventral canal nucleus in Sequoia.

The ventral canal nucleus remains closely applied to the surface of the egg and is somewhat flattened or compressed. It does not go through the peculiar changes which occur in the egg nucleus before fertilization, but having reached the condition shown in *fig. 90* does not develop much further until after the fertilization of the egg. It is furnished with a chromatin reticulum and an evident nucleolus. The ventral canal nucleus has usually been described as undergoing disorganization soon after its formation, sometimes reaching a resting condition, but generally never developing further than the first stages of this condition (Blackman, '98; Ikeno, '98; Murrill, '01, among others). Chamberlain ('98) figures a well-developed nucleus in the young fertilized archegonium of *Pinus Laricio*, which closely resembled the egg nucleus and which is, as he suggests, in all probability the ventral canal nucleus. Very recently Ikeno ('01) has described a large nucleus in the tip of the egg of Ginkgo and called it a ventral canal nucleus. He also calls attention to the possibility that a persistent ventral canal nucleus may have been mistaken for the extra male nucleus among previous observers. It has also probably been figured as the functional male nucleus.

The position of the ventral canal nucleus in Taxodium at some protected place on the side of the archegonium has preserved it from destruction during the entrance of the sperm cell, and as the fusing male and female nuclei approach the base of the archegonium the ventral canal nucleus begins to extend into the center, and by amitotic division it usually gives rise to the several nuclei of different sizes which occupy the upper half of the egg (*figs. 107, 112*). If the egg is not fertilized, the ventral canal nucleus generally remains unchanged in its original position (*fig. 107*), but it not infrequently increases in size and moves

nearer the center of the egg at about the time that those of the fertilized archegonia are dividing amitotically. In these cases it does not divide, but increasing greatly in size comes to resemble the egg nucleus just as in the case described by Chamberlain ('98) (*fig. 114*). Indications of amitotic division may be sometimes seen in the ventral canal nucleus in unfertilized archegonia (*fig. 113*), but such cases are rare. The development of the ventral canal nucleus in fertilized archegonia is not the exception, but the rule. In almost all cases in which there is a proembryo present there are to be found in the upper part of the archegonium a varying number of nuclei of different sizes which have been derived from the ventral canal nucleus (*figs. 115, 116*). In some cases, as would naturally follow when the ventral canal cell is cut off far down the archegonium, the nuclei derived from it may occupy a position near the base, and consequently near the proembryo. *Fig. 118* is such a case. Here, the ventral canal nuclei are sharply distinguished from the nuclei of the embryo (only one of which is shown) by the entire absence of the starch sheath characteristic of the latter. The ventral canal nuclei are usually separated from the proembryo by a distinct area of disorganizing protoplasm, but they themselves seem to retain a part of the protoplasm at the tip of the archegonium which is not disorganized until much later (*fig. 116*).

DEVELOPMENT OF THE FEMALE NUCLEUS.

The female nucleus in its very young stages is shown in *figs. 88* and *89*. It develops more rapidly than the ventral canal nucleus and goes through the peculiar changes of structure which have already been described in more or less detail by others. The chromosomes spin themselves out into a reticulum which is apparently often arranged in a spiral form (*fig. 89*). A nucleolus begins to appear early. At the stage of *fig. 89* the nucleus is not yet furnished with a distinct membrane, but in *fig. 90* the wall has appeared. There is first seen at this stage a finely granular substance which has been called metaplasmic substance by Strasburger and some recent workers. From the subsequent behavior of this substance, it would be better described

as kinoplasm than as metaplasm, but as the former word is overworked I shall follow Chamberlain ('99) and speak of it as linin, from which it does not seem to differ. It is at first entirely distinct from the reticulum, and is only very slightly stained in Flemming's triple. The nucleolus increases in size and the linin granules become more abundant as the nucleus develops. The reticulum still remains perfectly distinct from the granular substance and stains a bright red in safranin. The nucleolus is of quite a different character from the nucleolus of the central cell previously described. It becomes larger and larger until, at the time of fertilization, it is very conspicuous (*fig. 100*). When deeply stained, it seems to be entirely homogeneous, but on washing out a fine alveolar structure is to be seen. This does not in the least recall the irregular compound nucleolus of the central cell, and from the entirely different behavior of these two nucleoli during cell division it is evident they are of a different nature. The large nucleolus of the egg nucleus may be called the plastin nucleolus, while that of the central cell is a chromatin nucleolus. The plastin nucleolus of the egg nucleus seems to loose its stain more easily at one time than at another, as it is frequently found almost colorless. This loss of staining quality may be due to fluctuations in the amount of plastin material inclosed in its honey-comb-like structure during the active stages of development. This seems more probable, as it is often found when unstained in a collapsed condition, a distinct but thin shell being always present.

At the time of fertilization the female nucleus may vary considerably in its structure. Sometimes the linin material remains finely granular up to the time of fertilization. In such cases it is easily distinguishable from the chromatin reticulum, which on account of the huge size of the nucleus is now relatively scarce. The large plastin nucleolus is always present and is not connected in any way with the reticulum. This is another character which distinguishes it from the chromatin nucleoli already described. It is more frequently the case that the linin substance of the nucleolus, before the entrance of the male nucleus, has become grouped into an abundant reticulum, upon which granules of

various sizes are deposited (*fig. 101*). The larger of these linin granules take the red stain, and thus become indistinguishable from the chromatin masses of the nucleus. At no stage in the development of the egg nucleus is it without a distinct reticulum. Whether the chromatin reticulum contracts to form separate chromatin masses or whether it remains as the coarser part of the reticulum shown in *figs. 100* and *101* seems uncertain.

Chamberlain ('99) and Blackman ('98) have minutely described the development of the female nucleus in *Pinus Laricio* and *Pinus sylvestris*, respectively. The former describes the complete disappearance of the nuclear reticulum at two stages of the development of the nucleus. At the time of fertilization the chromatin is all grouped in the center of the egg nucleus, the remainder being occupied by the finely granular linin substance. This condition would not be so different from the case in Taxodium if the chromatin reticulum of the latter should resolve itself into chromatin nucleoli before the organization of the linin substance into a distinct reticulum. Such a condition, however, has not been found. In the mature egg nucleus the number of small nucleoli which take the red stain with safranin is sometimes no larger than could be supplied by the chromatin of the nucleus, but when the linin substance becomes collected into large granules, which is not at all unusual, they also take the red stain and cannot easily be distinguished from the chromatin nucleoli. Their color, however, is usually a more purplish red than is the case with the chromatin nucleoli, and if the washing is continued they are the first to lose the reddish stain.

FERTILIZATION.

We left the pollen tube after describing the formation of the male cells. The divisions of the central cell of the archegonium and of the central cell of the pollen tube occur simultaneously, or almost so, in every case observed, and in this respect again resemble the Cupresseae (Strasburger, '79). Fertilization occurs in a very short time after the completion of these divisions. As stated in my previous note, both sperm cells may enter one archegonium, but this is by no means always the case, in fact

not generally so; and when it does occur it may be considered as a failure to secure the results aimed at. When several pollen tubes have reached the archegonial group (as many as five have been noticed) the entrance of two or more sperm cells into an archegonium is not unusual, but when the number of tubes is only one or two it less often occurs. Pollen tubes sometimes are so abundant that all cannot pass into the depression above the archegonial group. Some then remain in different positions around the tip of the prothallium, and are often to be seen unchanged after their more fortunate neighbors have fertilized the archegonia. The central cell of such pollen tubes often divides at the same time with those over the archegonia, but in some cases where they are small and badly nourished the central cell does not divide at all.

In addition to the one or two sperm nuclei that enter the archegonium the disorganized remains of the stalk and tube nucleus with their surrounding protoplasm are also swept in, along with what is left of the neck cells. Prothallial nuclei are also sometimes thrown in, and quite a collection of such heterogeneous material may often be seen in the archegonial tip above the protoplasm of the egg. Most observers who have described the discharge of extra sperm nuclei or vegetative cells into the fertilized archegonium have made no distinction between entrance into archegonium and entrance into egg. Webber ('97) says that several spermatozoids may enter a single archegonium in Zamia, but that only the one that is used in fertilization actually enters the cytoplasm of the egg, the others remaining above and free in the cavity of the archegonial tip. Ikeno ('01) calls attention to this point, and finds that in Ginkgo the supernumerary spermatozoids do not enter the cytoplasm of the egg, but remain distinct from it, even if actually pressed into its surface. He also mentions the possibility that certain nuclei in the tip of the archegonia, that have in previous cases been described as derived from the sperm cell, are probably the results of amitotic division of a persistent ventral canal cell. These observations of Webber and of Ikeno I can positively confirm in Taxodium. The supernumerary sperm cells remain separate from the cytoplasm of the

egg, and may be long distinguished as they slowly disorganize (*figs. 104, 110*).

The functional sperm cell in its course to the egg nucleus is shown in *figs. 100* and *101*. Its protoplasm becomes intimately connected with that of the egg, but its identity is not lost at any stage. The starch sheath still remains in close contact with the sperm nucleus, and as its boundary touches the wall of the female nucleus it spreads around it more and more, while the sperm nucleus in its center finally comes in contact with the nucleus of the egg (*fig. 102*). This starch sheath of the sperm nucleus furnishes the sheath which is characteristic of the fusion nucleus.

Strasburger has several times spoken of the sudden appearance of starch in the fertilized egg of the Cupresseae. In his *Neue Untersuchungen* (1884) he expresses surprise at this, because, as he says, the pollen tube here contains very little starch before fertilization. His description in Juniperus of the starch sheath appearing around the fusion nucleus immediately after its formation and the subsequent behavior of the two may be applied almost word for word to Taxodium. It seems probable, therefore, that starch may yet be found in the male cells of the Cupresseae.

The sperm nucleus before contact with the female has the same character as was noticed in the pollen tube. It is difficult to distinguish it from the protoplasm around it, but a central nucleolus and a scarce reticulum may be made out in the dense substance that completely fills the nucleus. When the sperm cell enters the egg its nucleus is not more than a fifth the diameter of the egg nucleus (*fig. 100*), but during its course to the latter the sperm nucleus enlarges somewhat (*fig. 101*), and just after contact the diameter of the two nuclei is about as one to two. The male protoplasm, with its inclosed starch, now completely infolds the egg nucleus until it becomes evenly distributed around it (*figs. 102, 103, 105*). The structure of the sperm nucleus begins to change immediately on contact with the egg nucleus. The linin substance becomes arranged into a reticulum staining deep blue with gentian, while the nucleolus seems to break up into a number of smaller granules which lie more or

less grouped, but frequently scattered in no definite position. They were not found to be definitely located near the point of contact between the two nuclei as described by Blackman ('98) and Chamberlain ('99). The fusion nucleus begins to move to the base of the archegonium, and its male and female elements can be easily distinguished until the base is nearly reached (*fig. 106*). This passing of the fusion nucleus to the base of the archegonium before division occurs has been described by Strasburger ('79, '84) in Juniperus and by Jäger ('00) in Taxus.

The partition between the two nuclei does not entirely disappear until immediately before the first division. *Fig. 119* represents the two nuclei just after the disappearance of the separating wall. The parts derived from each are still distinct, the denser part being the male. The reticulum of the sperm nucleus is arranged in a more or less radiating way, and that of the egg is also becoming thus arranged. The large plastin nucleolus of the egg nucleus may be found in all stages of fusion. In addition to the reticulum and plastin nucleolus there are also present numbers of chromatin nucleoli in each half of the nucleus. The spindle of the first division is derived entirely from the reticulum of the fusion nucleus.

The structure of the male or sperm cell of Taxodium and its behavior during fertilization are worthy of especial emphasis. The presence of large quantities of starch around its nucleus and the transfer of this starch, together with its protoplasm, to form a distinct layer around the egg nucleus, which later becomes separated from the protoplasm of the egg in the base of the archegonium to form the greater part of the young embryo, are peculiarities not as yet described in any other organism, and they seem of sufficient interest to receive attention in any comparative study of sexual cells.

All observers who have studied fertilization in the gymnosperms seem agreed that the male nucleus slips from its protoplasmic sheath as it approaches the egg nucleus and leaves it behind near the point of entrance. If the case is as they think, Taxodium is an exception here.

In his well-known work on chromatophores, leucoplasts, etc.,

A. F. W. Schimper demonstrates the presence of plastids in the egg cells of plants. Taking the occurrence of starch as an indication of the presence of leucoplasts, we find that most of the plastids of the proembryo of Taxodium are furnished by the male cell. Occasionally a few scattered starch grains may be seen in the archegonium before fertilization, but as a rule the egg protoplasm is entirely free from them at maturity. Chromatophores or leucoplasts might of course be present in the egg without the occurrence of starch, and as such bodies are rather difficult to demonstrate without special methods, their presence cannot be denied. Blackman's ('98) observation of leucoplasts in the male cell of Pinus has already been referred to.

THE EMBRYO.

Fig. 120 shows an early stage in the formation of the spindle of the first division. The reticulum has become less coarse, the larger granules seeming to become transformed into smaller ones which characterize the fibers of the spindle at this stage. The outlines of the fusion nucleus are still quite distinct, and its fibers pass into those of the spindle imperceptibly. The chromatin has become arranged on the more homogeneous fibers in the center, and form ill-defined, much-elongated bodies which are not yet grouped into a definite plate. It will be seen that the spindle is multipolar at its origin. Stages of older spindles were not found.

The plastin nucleolus derived from the egg nucleus does not disappear during the spindle formation or during division of the nucleus. It is generally inclosed in one of the daughter nuclei, but is sometimes left free in the surrounding cytoplasm. The two daughter nuclei of the first division are first separated a considerable distance (*fig. 121*), but later approach nearer and are surrounded by the same starch sheath (*fig. 117*). Their structure is very similar to that of the egg nucleus before fertilization, a plastin nucleus, a chromatin reticulum, and a large amount of finely granular linin material being present. As the fusion nucleus approaches the base of the archegonium, it may rotate so that the part derived from the sperm nucleus lies nearest the base of the archegonium (*fig. 106*). The large vacuole of the

egg becomes broken up into smaller ones as the fusion nucleus approaches it, and in some cases almost disappears; often, however, the distinct starch-containing protoplasmic sheath of the fusion nucleus or its daughter nuclei is surrounded on both sides by large vacuoles (*fig. 117*).

The two daughter nuclei of the first division very soon prepare for the second division. *Fig. 122* shows such a nucleus in an early stage of mitosis. The chromatin is arranged in distinct rods, the linin granules have formed the reticulum, and the large plastin nucleolus is conspicuous. *Fig. 123* represents a late anaphase in the spindle of the second division. The number of chromosomes is evidently greater than in the division of the central cell. At this time the distinctive protoplasm of the proembryo has filled the base of the archegonium and is becoming more and more distinct from the ordinary egg cytoplasm above it. During this division and the one following, the plastin nucleolus is frequently left outside of the daughter nuclei, and may be broken up into several parts which lie free in the cytoplasm. *Fig. 124* gives the usual arrangement of the first four nuclei of the proembryo. They lie tetrad-fashion in the base of the archegonium, and a narrow zone of disorganizing protoplasm is beginning to appear above the starch-containing sheath around them. The cytoplasm is arranged in radiating lines from the nuclei. In *fig. 126* the third division has taken place. Several plastin nucleoli are present in the cytoplasm. In *fig. 125* the four nuclei of the second division are arranged in an unusual manner. They lie in one plane at the base of the archegonium and are bounded above by a large vacuole.

Spindles of the third division do not have any definite arrangement in reference to each other or to the axis of the archegonium, but their position seems to depend a good deal upon the width of the archegonium. After the formation of the daughter nuclei, however, these become arranged as *fig. 116*. Two are situated side by side at the base, and six lie above them in one plane. While this is the usual arrangement, it is not uncommon to find only one at the base, while the other seven are arranged above it. In a few cases there were three below

and five above. An abnormal condition is shown in *fig. 128*. Here two of the eight nuclei produced by the third division have not joined in the formation of the basal group, but remain some distance above, quite separate from the proembryo beneath. Two nuclei are at the base in this case, as usual, but the number above is only four, thus making up the total eight. All these nuclei are in division. The section is somewhat oblique, so that the base of one of the upper cells is shown above the two basal cells.

After the cells are arranged as mentioned, they become separated from each other by delicate cell walls, the upper tier remaining open at the top. The fourth division now takes place almost simultaneously in all of the nuclei. The axes of the spindles in the upper tier are parallel with the axis of the archegonium (*fig. 127*). There is thus cut off from the upper cells an equal number of nuclei which lie free in the cytoplasm of the egg and form the rosette (*fig. 129*). Cell walls are produced by this division and the middle tier is now completely closed (*fig. 129*). By referring to *fig. 127* it will be seen that the starch is all grouped in the base ends of the upper tier of open cells, and that the lower poles of the spindles are imbedded in it. When walls are formed all the starch is inclosed in the middle tier with the exception of a few scattered grains in the tip cells. The spindles in the lower cells lie at right angles to the ones above, and form a tier of four cells, or of six in those cases where three original cells have been arranged at the tip, or only two where there is but one tip cell. The middle tier now elongates into the suspensors (*fig. 133*), the nuclei and most of the cytoplasm appearing at the lower end. Further division in the tip cells does not occur until the suspensors have greatly elongated.

The formation of the embryo proper shows much variation. The suspensors from a single archegonium only rarely remain completely united at their tips, but usually separate more or less. The supernumerary suspensors are left behind at various positions, so that at the time of the first division of the tip cells the number of suspensors and tip cells is usually the

same. Each tip cell divides independently of the others, even when they are near together, and different stages of development are found in embryos from the same archegonium. Generally the tip cells are separated by the spreading or unequal growth of the suspensors. *Fig. 143* shows two embryos from the same archegonium, each with its own suspensor. In *fig. 144* the embryo and suspensor shown are situated at a considerable distance from any others.

Figs. 140–142 are serial sections through a group of embryos from one archegonium. There are four in the group, only three of which are shown. It will be seen that the growth in each proceeds independently, and some of them are more advanced than others. In *fig. 139* a two-celled and a three-celled embryo are represented. The first wall is almost always inclined and produces two cells generally of unequal size. The second wall arises in the distal larger cell, and is nearly at right angles to the first. The following divisions cannot be systematized by any rule, but, as will appear from the figures, are irregularly disposed. *Fig. 135* shows a suspensor bearing two embryos on its tip. It was teased from a prothallium and mounted whole. *Fig. 136* is a more magnified view of its tip; the two embryos are proceeding each on its own course in spite of the close contact of their original walls. In *fig. 146* the more advanced embryo seems to be formed of three distinct parts which may be interpreted as derived from three separate tip cells which proceeded alone in their development for a time, but being closely associated have united to form a single embryo. In *fig. 145* a single suspensor bears a single embryo. The embryonal tubes have appeared, but are not quite so much developed as in *fig. 146*. In *fig. 147* is shown the most advanced stage obtained of the young embryo. The embryonal tubes are very numerous and extend about four times farther up than is shown in the figure. They have completely filled the space previously occupied by the suspensor, of which no trace can be seen at this time. Three abnormal embryos are shown in *figs. 130–132*.

From this description it will be seen that the development of the embryo of Taxodium differs from all other conifers. In

Taxus (Jäger, '99) and Cephalotaxus (Arnoldi, '00) there are more than eight free nuclei present before cell formation, and the tiers are not so definite as in Taxodium. In the Cupresseae (Strasburger, '72) the tiers are at first composed of single cells, while in the Abieteae only one tier is first formed which then gives rise to four by successive divisions. Coulter ('97) and Coulter and Chamberlain ('01) have described peculiarities in the number of embryos formed from one archegonium, and in the relation of suspensors to embryos in *Pinus Laricio*, which are not unlike the diversities found in Taxodium.

SYSTEMATIC POSITION OF TAXODIUM.

The family Taxodieae as arranged by Eichler is acknowledged a tentative one, and when we compare the gametophytes of Sequoia and Taxodium, the only two genera of this family in which this part of the life history has been followed, we are impressed, not with similarities, but with divergencies; and it becomes at once apparent that, if gametophytic characters are of any consequence in classification, the group as it now stands is an artificial one and must be rearranged. The points of divergence between Taxodium and Sequoia are so striking that to retain them longer in the same group would do violence to taxonomic principles. In the large number of functional megaspores and prothallia present in its sporangia Sequoia is markedly primitive, and in the arrangement and number of its archegonia it is, so far as known, *sui generis*. Its male gametophyte is imperfectly known, the young stages being quite unstudied.

In the preceding pages attention has been called in passing to certain of the more evident structural similarities between Taxodium and the Cupresseae, and for the sake of brevity they will not again be rehearsed here. It is sufficient to say that Taxodium agrees with the Cupresseae in all gametophytic characters that seem to me of much taxonomic importance, and I think it evident that such essential agreement with the Cupresseae on the one hand and such fundamental divergence from Sequoia on the other must necessitate the removal of Taxodium from its connection with the latter and its insertion in the former family.

Such a change will require us to discard the name Taxodieae and combine the remaining genera of the family into some tentative group of another name until further study shall make their position clear.

SUMMARY.

The staminate cones begin to develop in September or October, and by winter the pollen mother-cells are formed. In spring starch is removed from the cells of the sporophyll and stored in the mother-cells, where it remains through their divisions and disappears in the pollen grain as the exine is being formed. The exposed wall of the microsporophyll is but two layers thick.

The reducing divisions in the pollen mother-cells resemble those in the Larix and the reduced number of chromosomes is probably twelve. There is a fairly well developed resting stage after the first division in the mother-cells.

About ten days after the reducing division a division of the pollen grain occurs which separates at once the generative cell from the tube cell. No sterile prothallial cells are formed.

From two to three weeks after pollination, when the pollen tube has grown some distance, the generative cell divides into the central cell and stalk cell, and these move down toward the tube nucleus. The pollen tube reaches the prothallium earlier than in any case previously described; sometimes even before the formation of a cellular tissue in the latter.

The arrangement of the nuclei in the pollen tube is the same as in other conifers.

The central cell has a distinct *Hautschicht* of its own and resembles in outline that of Taxus and the Cupresseae. It divides simultaneously with the division in the central cell of the archegonium, and the two sperm cells thus formed move apart slightly. They are furnished with a dense layer of starch around the nucleus, a peripheral finely granular layer often containing globules of plastic material, and a *Hautschicht.* Its nucleus is densely filled with granular material and has a coarse chromatin recticulum and a nucleolus.

The ovulate cones also begin their development in early fall and continue growing slowly, as the weather permits, through

the winter. At the time of pollination the single megaspore mother-cell may be distinguished. It is filled with starch, as are also the tapetal cells around it. Two reducing divisions occur, but only three cells are formed, the upper of the two first produced not dividing again. The lower of the two potential megaspores resulting from the second division in the lower cell develops into the female gametophyte, the two upper cells disorganizing.

As the spore develops in sprouting, the tapetal cells around it grow and divide, and disorganizing the nucellar cells around them pass the nourishment to the prothallium within. How long this tapetum persists is not certain, but it probably lasts until the prothallium is mature.

The archegonia are arranged as in the Cupresseae. The number of the neck cells vary from two to sixteen or more. The central cell is very long and contains two conspicuous kinoplasmic areas, one at the upper end near the nucleus and the other in the lower end beneath the large central vacuole. When the ventral canal nucleus is cut off the upper of these masses takes part in the division, while the fragmented lower one fills the base of the archegonium with peculiar figures.

A ventral canal nucleus is cut off just before fertilization, but it is not separated from the cytoplasm of the egg and after fertilization moves back toward the center and divides amitotically. It probably assists in nourishing the embryo.

The spindle of the ventral canal cell division is almost entirely of nuclear origin, and the chromosomes are derived largely from the nucleolus. The egg nucleus contains a large amount of granular material, but a chromatin reticulum is always present. This granular material is largely used in the formation of the spindle of the fusion nucleus.

Fertilization occurs about the middle of June, and two or more sperm cells may enter an archegonium. Only one, however, becomes fused with the egg cytoplasm. As a rule one pollen tube fertilizes two archegonia.

The sperm cell with its starch, protoplasm, and nucleus passes through the cytoplasm of the tip of the egg and reach-

ing the female nucleus enfolds it. Its starch is uniformly distributed around the fusion nucleus and passes with it to the base of the archegonia to be included in the cytoplasm segregated off as the proembryo. The larger part of the cytoplasm of the egg takes no direct part in the formation of the embryo, but is digested and used by the latter in its growth.

The first division occurs after the fusion nucleus has reached the base of the archegonium.

Eight free nuclei are formed, which arrange themselves in two tiers, the upper of which generally contains six, the lower two. Cell walls are now formed, but the upper side of the upper tier is left open. This open tier now divides by walls at right angles to the long axis of the archegonium into the rosette of free nuclei above and the suspensors below. The two cells of the lower tier divide at the same time by walls parallel to the long axis of the archegonium, and thus four cells instead of two are produced in one plane.

The suspensors as they elongate may or may not separate, and thus one or several embryos may be formed from one archegonium.

It is thought that the family Taxodieae as now composed is an artificial one; that Taxodium itself must be removed to the Cupresseae, leaving Sequoia and perhaps other as yet imperfectly known genera of the present family Taxodieae to be included in a family of their own under another name.

NOTE.

Since the completion of this work in May, 1901, several papers have appeared bearing more or less closely on certain points here taken up. Miss Ferguson's two papers on fertilization, etc., in Pinus (Annals of Botany, 1901), and Arnoldi's *Beiträge zur Morph. de Gymn.* V. (Bull. Soc. Imp. Nat. Moscow, No. 4, 1900), dealing with fertilization, embryo formation, etc., in the "Sequoiaceen," are important, and would have been referred to frequently in the text had they appeared before this work was handed in. Miss Ferguson confirms Blackman's ('98) statement that the sperm cells of Pinus are furnished with a cyto-

plasm of their own, though the outline of the cell seems to be neither so regular in shape nor so definite in outline as in other groups of gymnosperms. She finds no starch in the male cells, although much is present in the pollen tube. Miss Ferguson also suggests that the "spongy" tissue is useful in nourishing the prothallium, and brings out other interesting points, which must, however, be passed by here.

Arnoldi, in the communication mentioned, finds starch in the sperm cells of Sequoia, Cryptomeria, and Taxodium, and notes its transference to the embryo. He also considers necessary the removal of Taxodium (and several other genera) into the Cupresseae; but on certain points of fact in developmental processes our work does not agree.

In the recent Belfast meeting of the British Association Mr. Harold Wager presented a paper on the function of the nucleolus, in which he is reported as finding that "this body, in the cases examined by him, appears to be intimately connected with the nuclear network, and contains chromatin material which contributes directly to the formation of the chromosomes" (Nature **67**: 20. 1902). These results are of interest in connection with my conclusions.

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EXPLANATION OF PLATES I–XI.

The abreviations used are: *st*, stalk cell or stalk cell nucleus; *gr*, generative cell; *ptn*, pollen tube nucleus; *cc*, central cell of pollen tube; *sct*, sclerenchymatous cells; *vcn*, ventral canal nucleus; *en*, egg nucleus.

PLATE I.

FIG. 1. Median longitudinal section through young microsporangium; primary archesporium evident as rows of cells. × 400.

FIG. 2. Microsporangium in October; tapetum differentiated. × 300.

FIG. 3. Spindle of first division of microspore mother-cell. × 800.

FIG. 4. Anaphase of same, showing four limbs to chromosomes. × 800

FIGS. 5–6. Chromosomes seen from poles as they approach them; eleven in *fig. 11.* × 800.

FIG. 7. Spindle of second division; mother-cell walls not yet dissolved. × 800.

FIG. 8. Microspore before first division; cell wall not shown. × 800.

FIGS. 9–11. Successive stages in first division of microspore. × 800.

FIG. 12. Pollen grain on tip of nucellus, exine split off. × 800.

FIG. 13. Pollen grain beginning to germinate, exine split off and generative cell swelling out. × 800.

FIG. 14. The same; young stage of germination. × 500.

FIG. 15. Tube nucleus moving down. × 500.

FIG. 16. Different relative position of generative cell and pollen tube than in above. × 500.

FIG. 17. Indication of branching in pollen tube. × 500.

FIG. 18. Generative cell just before commencing to divide. × 800.

FIG. 19. Generative cell immediately after division. × 800.

FIG. 20. Pollen tube with three nuclei. × 280.

FIG. 21. Central and stalk cell of same tube more magnified; stalk cell protoplasm beginning to merge into that of pollen tube. × 800.

FIG. 22. All three nuclei moving down, and close together. × 400.

FIG. 23. Pollen tube slightly older; stalk nucleus has passed central cell and lies by tube nucleus from which it differs in its smaller size; May 15, 1900. × 400.

PLATE II.

FIG. 24. More developed pollen tube; stalk and tube nuclei alike. × 235.

FIG. 25. Tip of ovule; pollen tube has reached megaspore in which no cell walls have yet formed. × 26.

FIG. 26. Tip of pollen tube that has reached the prothallium; nuclei in usual position. × 400.

FIG. 27. Central cell of pollen tube shortly before division; one free nucleus shown. × 800.

FIG. 28. Central cell preparing to divide; free nuclei and protoplasm of pollen tube disorganizing. × 400.

FIG. 29. Spindle of division of central cell. × 800.

FIG. 30. Telophase of the same. × 400.

FIG. 31. Sperm cells separated from each other. × 400.

PLATE III.

FIG. 32. Megasporophyll with the axillary megasporangium rudiment just beginning to show; Oct. 3, 1899. × 95.

FIG. 33. The same; integument beginning to appear; Jan. 4, 1900. × 95.

FIG. 34. Little older megasporophyll and ovule; March 11, 1900, Baltimore. × 95.

FIG. 35. The same; ready for pollination; megaspore mother-cell not yet divided; March 31, 1900. × 80.

FIG. 36. Longitudinal section of sporangia and sporophyll ten days after pollination; placenta now beginning to appear above the ovule; April 3, 1901. × 36.

FIG. 37. Sporophyll and ovule about three weeks after pollination; micropyle closed and placenta becoming prominent; April 22, 1900. × 36.

FIG. 38. Megaspore mother-cell before division. × 800.

FIG. 39. The same; in synapsis. × 1030.

FIG. 40. The same; spindle of first division. × 950.

FIG. 41. The same; older spindle of first division. × 950.

FIG. 42. The same; wall being formed. × 950.

FIG. 43. The same; spindle of second division. × 950.

FIG. 44. Megaspore with the two disorganizing spores above. × 950.

PLATE IV.

FIG. 45. Megaspore before first division; distinct zone of large cells around it. × 400.

FIG. 46. Two cells of the large-celled tissue in division. × 800.

FIG. 47. Germinating megaspore in middle of large-celled tissue; April 29, 1900. × 70.

FIG. 48. Enlarged section of the above-mentioned tissue. × 400.

FIG. 49. Longitudinal section of entire ovule five weeks after pollination. × 36.

FIG. 50. Ovule showing two prothallia. × 70.

FIG. 51. Longitudinal section showing nucleated cytoplasm of wall layer of megaspore, large-celled tissue, and nucellus cells. × 400.

FIG. 52. Large-celled layer around somewhat older prothallium. × 280.

FIG. 53. The same; after-formation of prothallial cells. × 280.

FIG. 54. Young stage, ingrowing cells of prothallium. × 280.

PLATE V.

FIG. 55. Prothallial tubes, after closure of inner ends. × 280.

FIG. 56. Two-celled stage of the same. × 280.

FIG. 57. Tip of young prothallium showing group of archegonium initial cells. × 70.

FIG. 58. Prothallial cell becoming multinucleate. × 400.

FIG. 59. The same with five nuclei. × 400.

FIG. 60. Formation of neck cells in archegonia. × 280.

FIG. 61. Older archegonium; neck cell divided. × 280.

FIG. 62. Still older archegonium; kinoplasmic areas beginning to appear. × 280.

FIG. 63. Nucleus of central cell of archegonium at same age as above. × 400.

FIG. 64. Group of archegonia showing ten in one section, two pollen tubes above; somewhat diagrammatic. × 70.

FIG. 65. Cross-section of group of archegonia, showing seventeen. × 85.

PLATE VI.

FIG. 66. Archegonium showing kinoplasmic masses in central cell; after entrance of plastic stuff from neck cells. × 280.

FIGS. 67–69. Jacket cells in normal activity. × 800.

FIG. 70. Spindle in jacket cell at time of fertilization. × 800.

FIGS. 71–74. Stages of disintegration of nuclei of jacket cells. × 800.

FIG. 75. Lower part of archegonium at time of fertilization showing proteid vacuoles. × 800.

FIGS. 76–82. Successive stages in division of central cell of archegonium; *fig. 76.* × 400; *figs. 77–82.* × 800.

PLATE VII.

FIGS. 83–90. Successive stages in division of central cell of archegonium; *figs. 83–89.* × 800; *fig. 90.* × 280.

FIG. 91. Group of archegonia after formation of ventral canal nuclei. × 36.

FIG. 92. Two archegonia of same group slightly more magnified. × 70.

FIGS. 93–96. Neck cells seen from above. × 400.

FIGS. 97–98. Surface view of megaspore wall showing pits; after formation of young prothallium. × 800.

FIG. 99. Pits of same wall in section. × 800.

PLATE VIII.

FIG. 100. Sperm cell just entering cytoplasm of archegonium tip; its nucleus barely visible in dense starch sheath around it. × 800.

FIG. 101. Sperm cell protoplasm just touching egg nucleus; sperm nucleus not yet in contact with egg nucleus. × 800.

FIG. 102. Sexual nuclei in contact; sperm cell protoplasm beginning to inclose the egg nucleus. × 400.

FIG. 103. Later stage of fusion. × 400.

FIG. 104. Supernumerary sperm cell in tip of archegonium. × 400.

FIG. 105. Later stage of fusion; starch sheath completely inclosing the not yet entirely fused nuclei. × 400.

FIG. 106. Archegonium at the stage above; fusing nuclei moving down and large vacuole broken up. × 70.

FIG. 107. Egg and ventral canal nucleus in tip of an archegonium that did not get fertilized. × 280.

FIG. 108. Ventral canal nucleus at tip of an archegonium of same group as above which has been fertilized and has a two-celled embryo in the base. × 280.

FIG. 109. Ventral canal nucleus in another fertilized archegonium of same group; it has grown out into the protoplasm and is beginning to divide amitotically. × 280.

FIGS. 110–112. Successive stages in growth of ventral canal nucleus in fertilized archegonia; all with young embryos in base; extra sperm cell lying in tip of archegonium in 110. × 400.

PLATE IX.

FIGS. 113–114. Ventral canal cells in archegonia that missed fertilization; others in group have been fertilized. × 280.

FIG. 115. Amitotic division of ventral canal nucleus. × 400.

FIG. 116. Archegonium with 8-celled embryo at base; wells are formed between the cells, but upper cells open above; here there are seven cells in upper tier and only one below; canal nucleus at tip; disorganized layer above embryo. × 400.

FIG. 117. Archegonium with two-celled embryo near base; ventral canal nucleus in division above, and second sperm cell free in tip. × 280.

FIG. 118. Ventral canal nucleus divided, lying at base of archegonium in contact with two-celled embryo, only one of the nuclei of which is shown; embryo surrounded by its starch sheath. × 400.

FIG. 119. Late stage of fusion of sperm and egg nuclei. × 800.

FIG. 120. Spindle of first division of fusion nucleus; large plastin nucleolus unchanged. × 800.

FIG. 121. Two daughter nuclei of fusion nucleus, immediately after division. × 800.

FIG. 122. Preparation for second division. × 400.

FIG. 123. Spindle of second division. × 800.

PLATE X.

FIG. 124. Four-celled embryo; nuclei in usual position, two above and two below arranged tetrad fashion. × 280.

FIG. 125. Embryo of same stage as above, nuclei all arranged at base in one plane. × 280.

FIG. 126. Spindles of third division; plastin nuclei in protoplasm. × 280.

FIG. 127. Eight-celled embryo, six cells above and two below; the upper are dividing, the lower preparing to divide. × 280.

FIG. 128. Abnormal embryo, cut a little obliquely; two of the nuclei have not joined in the tier formation, but have remained a little distance above, and in dividing only one is shown; the other lies beside it in another section. × 280.

FIG. 129. Sixteen-celled embryo in three tiers; six cells in rosette, six suspensor cells, and four below. × 280.

FIGS. 130–132. Abnormal embryos. × 280.

FIG. 133. Sixteen-celled embryo after suspensors have lengthened considerably. × 280.

FIG. 134. Cross-section through a group of seven suspensors. × 400.

FIG. 135. A single suspensor carrying two embryos which are developing separately. × 29.

FIG. 136. Tip of above suspensor with its two embryos more magnified. × 400.

FIG. 137. A two-celled and a three-celled embryo, each on its own suspensor. × 280.

PLATE XI.

FIG. 138. Two four-celled embryos; there are four embryos in the group and four suspensors; three of the embryos are four-celled, and one about six-celled. × 280.

FIG. 139. A three-celled and an about eight-celled embryo; four embryos in group and three suspensors. × 280.

FIGS. 140–142. Three consecutive sections through a group of four

embryos hung by three suspensors; the fourth embryo does not appear in these sections. × 280.

FIG. 143. Two embryos, each on its own suspensor; they are from the same archegonium; there are two others in the group. × 280.

FIG. 144. One embryo on one suspensor, off to itself. × 280.

FIG. 145. Older embryo on much enlarged tip of suspensor; embryonal tubes beginning to appear. × 280.

FIG. 146. Apparently three embryos of a group uniting to form a single embryo; embryonal tubes conspicuous. × 280.

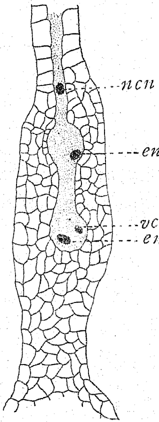
FIG. 147. Older embryo; embryonal tubes extend up about four times as far as shown. × 280.

BRIEFER ARTICLES.

THE OCCURRENCE OF TWO VENTERS IN THE ARCHEGONIUM OF POLYTRICHUM JUNIPERINUM.

THE interesting phenomenon of a double venter in the archegonium of *Polytrichum juniperinum* was observed, in material sectioned and studied by the writer, in a course of comparative morphology and embryology of plants under the direction of Dr. Margaret C. Ferguson, of Wellesley College.

The archegonium illustrated in the accompanying figure shows two distinct venters, the lower venter containing two nuclei, which probably represent the egg cell and the ventral canal cell. The upper venter has doubtless been developed from the first neck canal cell and contains but a single nucleus. Directly above, in the neck of the archegonium, is the nucleus of the second neck canal cell.



Base of archegonium of *Polytrichum juniperinum* showing two venters.

Previous to the time that these observations were made, no similar phenomenon had been noted as occurring in the archegonium of the Musci, but, while preparing this note for publication, the February number of the BOTANICAL GAZETTE appeared, in which the "occurrence of two egg cells in the archegonium of Mnium" was described by Coker.[1]

There are two opinions held today regarding the origin of the neck canal cells. According to Campbell,[2] the neck canal cells are derived from the terminal cell cut off from the mother-cell of the archegonium, while Gayet[3] maintains that, in the Musci as in the Hepaticae, the terminal cell does not give rise to the neck canal cells, but that

[1] COKER, W. C., On the occurrence of two egg cells in the archegonium of Mnium. BOT. GAZ. 35: 136. 1903.

[2] CAMPBELL, D. H., Mosses and ferns 194. 1895.

[3] GAYET, L. A., Recherches sur le développement de l'archegone chez les Muscinées. Ann. Sci. Nat. Bot. VIII. 3: 161–258. 1897.

they are derived from an initial cell cut off from the mother-cell of the oosphere. It would seem from the recent observations of two egg cells in the archegonium of Mnium and of Polytrichum that the neck canal cells are potential egg cells, and as such argue for Gayet's theory that the egg cell and neck canal cells have a common origin.—MARY C. BLISS, *Wellesley College.*

POLYEMBRYONY IN GINKGO.

IN the BOTANICAL GAZETTE 34:64, July 1902, I published a short note on the polyembryony of Ginkgo. Since polyembryony is of rather common occurrence among the gymnosperms, its frequency in Ginkgo becomes a point of some interest. Through the kindness of Dr. George T. Moore and Mr. Carl Kellerman, of the Department of Agriculture, I have secured a number of seeds of the Ginkgo. A careful examination of two hundred specimens give the following results: 12 per cent. were without embryos, while 2 per cent. showed two small but well-formed embryos in each seed. In the cases of polyembryony the embryos averaged about one-third the length of the single embryos. With one exception, the double embryos were approximately the same length; in this case one embryo was about twice the length of its fellow. The single embryos showed great variation in length, but the short ones were always thicker than the long ones. One embryo had three well-developed cotyledons. — MEL. T. COOK, *De Pauw University, Greencastle, Ind.*

CURRENT LITERATURE.

BOOK REVIEWS.

Plant physiology.

PROFESSOR G. J. PEIRCE, of Stanford University, has elaborated lectures upon plant physiology which he has been giving in the University into a text-book,[1] less extensive than Pfeffer's treatise, and more full than Noll's treatment in the Bonn text-book. This is published in attractive form and will be found of interest both to the general reader and to students. The book differs from the *Text-book of plant physiology* by MacDougal, in that there are no laboratory directions, the author believing that the laboratory manual and the text should be divorced. The only English work with which the book at all competes is the *Vegetable physiology* of Professor J. Reynolds Green.

Peirce's book shows strongly the impress of Pfeffer's *Physiology*, and to him the author makes ample acknowledgment. One who reads the book carefully will be impressed by the clearness of style and the vigor of presentation, as well as by the freshness of much of the matter and the modern point of view from which the author regards his subject. The book is characterized by two features: first, an endeavor to state the phenomena of plant life in the terms of physics and chemistry; and, second, by the clear recognition of the fact that very many plant phenomena cannot yet be adequately stated in these terms, and the consequent acknowledgment that they are at present not sufficiently known. This makes the book stimulating to the student, for many lines along which research will be profitable are pointed out to him. In many ways the book is a decided advance upon any English text which has come to our notice.

After recognizing fully the value of this work, its originality, its vigor, its clearness, its stimulating statements of the incompleteness in our knowledge, and its probable marked usefulness as a text-book in colleges and schools, there remains the less pleasant task of pointing out some of its shortcomings.

After an introductory chapter, the first topic is respiration, and here we think the author has adopted an unfortunate theory which does not agree with the observed phenomena. The whole treatment is based upon the theory that foods of various kinds are directly oxidized to furnish energy. This is plainly derived from Pfeffer, and of course should be stated as a theory; but the other view of respiration, which, in our judgment, is much more probable because in closer harmony with the facts, is not even mentioned.

In the chapter on nutrition which follows, there is no adequate treatment

[1] PEIRCE, GEORGE JAMES, A text-book of plant physiology, 8vo. pp. vi + 291, *figs. 22.* New York: Henry Holt and Company. 1903. $2.00.

of the mode of absorption of gases, which is repeatedly spoken of as though it were merely their diffusion from the external air into the intercellular spaces.

We are glad that Professor Peirce adopts the view that the food of all plants consists of complex carbon compounds ; but he does not always in his terminology distinguish between foods and the materials out of which green plants may construct foods. Assimilation is very properly distinguished from photosynthesis. The treatment of the latter might have been somewhat extended with profit. It would have been especially desirable to include some notice of the work of Friedel (1901) on extracellular photosynthesis, especially as that work was confirmed in the autumn of 1902 by Macchiati.

It would seem that the chapter on absorption and movement of water might have been advantageously placed at the beginning of the book, since such processes are fundamental to an understanding of respiration or nutrition. The discussion of absorption, transfer, secretion, etc., are in the main clear and in accordance with modern physical notions, though there are some slips that should be corrected in later editions, such as the definition of osmotic pressure. In the treatment of transpiration and the movement of gases, however, the author has not freed himself from older and untenable ideas. This is well illustrated by the sentence: "It may easily happen in temperate regions that the plant takes in more water and more salts than it really needs, and that while the former evaporates, the latter accumulate in useless forms and quantities, with or without chemical change." Similarly, the account of gas exchanges in the intercellular spaces is open to serious criticism.

We fear that readers will be somewhat puzzled in the chapter on growth by such contradictory statements as these: "Growth is a process dependent upon the formation of new protoplasm" (p. 165); "The second stage in growth . . . . consists mainly, if not wholly, in the absorption of water" (p. 167). On page 166 we have the formation of new protoplasm and new cells described as "the first and *fundamental* stage in the process of growth;" while on page 174 we are told, "Cell division . . . . does not constitute an essential part of the process of growth."

The treatment of the subject of irritability is distinctly novel and interesting. For the student, however, it lacks a logical presentation of the phenomena of irritability which are common to all its manifestations. The chapter on reproduction, which in many physiological books is merely an account of the morphological phenomena, is noteworthy in being almost purely physiological, and it makes very obvious how little we yet know about the physiology of reproduction. In this connection the author lays more stress upon the results of Klebs than future study is likely to justify, since Klebs omitted all consideration of the effects of osmotic pressure in the solutions with which he was working. It is not unlikely, therefore, that his conclusions will be profoundly modified when this factor is taken into account. Certainly the work of Livingston, Greeley, and others, points strongly in this direction.

That the topic digestion is nowhere treated is certainly a noteworthy omis-

sion. Only as an incident in the chapter on nutrition is it mentioned that foods temporarily stored in the chloroplasts must be transformed before removal, and implications of the same kind occur in connection with the general subject of the transfer of foods. But nowhere is there any discussion of the important part which digestion plays in plant life, nor any account of the agents by which it is accomplished.

It would not be difficult to point out minor inaccuracies here and there in Professor Peirce's book, nor unfortunate modes of expression; an illustration of the latter, and one very common in physiological writings, is repeated many times when he speaks of natural "laws" as though they were objective and efficient agents.

Professor Peirce's book contains so many excellent features that it is unfortunate to have it marred somewhat by sins of omission and commission. But all these matters may be rectified in future editions without fundamentally changing the character of the book, which will be useful to students, particularly if they have access to other books; and nowadays no student ought to get his physiological information from one source.—C. R. B.

Diffusion and osmotic pressure.

The rôle of diffusion and osmotic pressure in plants, by Dr. Livingston, is a well-made and attractive-looking volume of 149 pages, constituting one of the Decennial Publications of the University of Chicago.[2]

For several years the need of a concise, yet sufficiently detailed, statement of the facts and modern theories of diffusion and osmosis, on both the physical and the physiological side, has been felt by every student and teacher of physiology. Such a volume has now appeared.

Dr. Livingston has divided his book into two parts, one dealing with physical and the other with physiological considerations. In the first part we have Matter and its states, Diffusion and diffusion tension, Liquid solutions, Ionization, Osmotic phenomena, Measurement and calculation of osmotic pressure; and in the second part Turgidity, Absorption and transmission of water, Absorption and transmission of solutes, Influence of the osmotic pressure of the surrounding medium upon organisms.

After stating briefly the theories of matter, the author proceeds to the consideration of the diffusion of gases, liquids, and solids, and then in the following chapter discusses in a lucid manner the difficult subject of solutions, using this opportunity to repeat and apply the teachings of the preceding chapter on diffusion, and showing his regard for the needs of the student by defining such terms as *normal solution*, *gram-molecule solution*, and *gram-equivalent* solution.

[2] LIVINGSTON, BURTON E., The rôle of diffusion and osmotic pressure in plants. Decennial Publications of the University of Chicago, Second Series, Vol. VIII. 8vo. pp. xvi + 149. University of Chicago Press. 1903. $1.50.

A brief discussion of the ionization of gases and of solutes in solution opens the way for a very satisfactory presentation of the general subject of osmosis, wherein the osmotic pressure of non-electrolytes, electrolytes and colloids is treated, and the means and methods of measuring and calculating the pressure are set forth with appropriate formulas.

Having laid a foundation in the physical, the author proceeds to the still more difficult physiological. To this part nearly a hundred pages are given. Only a few of the more striking topics can be mentioned here. Plasmolysis is shown to be not a matter of simple interpretation, as one would infer from literature generally, but a thing to be judged only after the permeability of the protoplasmic membrane is known. To determine the permeability various tests are detailed. The action of the protoplasmic membrane and the maintenance of turgidity in spite of permeability are two of the most interesting because most difficult theoretical discussions. It is evident that the author inclines to the solvent theory as applied to the action of the membrane in osmosis. In the chapters on the absorption and transmission of water and solutes, the means of lifting the sap to the tops of trees, and the means of èxudation from water-pores, nectaries, etc., receive due consideration. These most difficult questions are not, as is too often the case, dismissed with the statement that there are no satisfactory explanations, but carefully and clearly the principal experimental results are recorded, their bearing pointed out, and their insufficiency noted. The pumping action of osmosis and the tensile strength of water are given as both probable means in the lifting of sap to great heights; while a change in the permeability of the protoplasmic sac is given as the possible cause of the beginning of excretion by water-pores and nectaries.

The last chapter represents in large measure original work by the author. Here are summarized his well-known experiments on the morphology of algae as influenced by the osmotic pressure of the surrounding medium. The work of Loeb, Massart, Rothert, and others, on the effect of osmotic pressure on irritability and in inducing parthenogenesis finds appropriate mention.

In the book as a whole there is little to criticise adversely and much to praise. Possibly the author pushes the theoretical a little too far sometimes, as, for example, in his explanation of the rise of a solution in a thistle-tube used as an osmometer. But it is better to state an insufficient hypothesis than to ignore all. In the reviewer's opinion one of the merits of the book is its abundance of theories clearly and boldly stated, while at the same time it points out the strength and weakness of each.

Pedagogically the treatment is excellent. The parts are well arranged, everything is interesting, a basis for the physiological is laid in the physical, there are copious citations of literature, and there are many suggestions as to problems for research. In the opinion of the reviewer Dr. Livingston has produced an excellent treatise.—FREDERICK C. NEWCOMBE.

White rot.

IN A SUMPTUOUS VOLUME of 300 pages, embellished by 24 elegant double colored plates, the Hungarian Department of Agriculture has published a detailed account of Dr. Gy. de Istvánffi's studies on the white rot of the grape (*Coniothyrium Diplodiella*).[3] The first part of the work is devoted to a minute description of the development of the disease, and the reactions induced in the host plant by the fungus. Of the latter the author distinguished four stages or degrees of injury occurring on the stems of American vines. The most interesting of these is the phenomenon termed "complete girdling" which is described at great length. The results produced are similar to the effects of artificial girdling. Further, the results of studies of the fungus in cultures and of artificial infections are described.

The most interesting part of the work is that which deals with the effects of various toxic substances on the fungus. A few examples are briefly given here. Vigorous mycelium from pure cultures was not injured by being immersed for 24 hours in a 2 per cent. copper sulfate solution, or in Bordeaux mixture made of 2 per cent. copper sulfate and 2 per cent. lime. When again transferred to nutrient solution the mycelium developed fruit in 18 to 20 days. On the other hand 2 per cent. cuprammonia or a mixture containing 0.192 per cent. $Ca(HSO_3)_2$ and 0.018 per cent. SO_2 proved fatal.

Again, parts of stems covered with pycnidia were plunged in various mixtures with a view of killing the spores in the pycnidia. When immersed in this way for 24 hours in a mixture of 0.288 per cent. $Ca(HSO_3)_2$ and 0.04 per cent. SO_2 the spores were killed. The same results were obtained with 10 per cent. sulfuric acid and with 10 per cent. sulfate of iron. When the stems were merely sprinkled with the same liquids the spores remained uninjured.

Further, spores developed in must containing 1 per cent. copper sulfate solution, only slightly in 2 per cent. solution, and not at all in a 3 per cent. A 0.3 per cent. solution of the calcium sulfite-sulfurous acid mixture proved fatal. These experiments were performed with a view of finding a method of combating the disease. The effect of such easily soluble and highly poisonous substances as the sulfurous acid mixture on living vines remains still to be determined.

It is remarkable that a work treating a serious fungous disease from an economic standpoint contains no record of field experiments for the control of the malady. The author's suggestions for combating the fungus are based mainly upon theoretical considerations and are for the most part impracticable, when not wholly at variance with long established principles of controlling fungous diseases.

[3] ISTVÁNFFI, GY. DE, Études sur le rot livide de la vigne (*Coniothyrium Diplodiella*). Ann. Inst. Ampélologique Royal Hongrois vol. 2. pp. vii + 288, *figs. 12*, *pls. 24*, double, colored. Budapest: Publications du Ministre Royal de l'Agriculture de Hongrie. 1902.

While the work is an excellent anatomical study of the fungus and its relation to the host, it contains little to elucidate the life-history of the fungus in nature, which, as the author remarks in the first chapter, is the only basis upon which defense is possible.—H. HASSELBRING.

MINOR NOTICES.

THE ACCOUNT of *Eucalyptus obliqua* L'Her., which is figured on four plates, forms part II of Maiden's *Critical revision of the genus Eucalyptus.* —C. R. B.

ENGELMANN has recently published the fifth fascicle of Dalla Torre and Harms's *Genera Siphonogamarum*,[4] including genera numbered 5183 to 6491.—C. R. B.

VOLUME 3 of the botanical series of the Field Columbian Museum is to be wholly devoted to *Plantae Yucatanae* by Dr. C. F. Millspaugh.[5] Dr. Millspaugh has been studying the plants of the insular, coastal, and plains regions of Yucatan for several years and has collected personally in this region. He has now begun the enumeration of the flora of the Antillean portion of Yucatan, which may be described as embracing roughly the portion of the state of Yucatan lying north of latitude 19° 30′. Fascicles will appear from time to time, as opportunity permits, without regard to the natural sequence of the orders, though they will be complete as far as the knowledge of the species permits. As a basis for the most important specific distinctions Dr. Millspaugh has selected the fruits and seeds, believing that these vary less than any others. Each species is illustrated by an inset figure, somewhat after the manner of Britton and Brown's *Illustrated flora*. These figures are admirably drawn by the author or by Miss Agnes Chase; unfortunately many of them have been sadly marred in the printing. If the copy which has reached us is a fair sample, we can only express surprise that the Museum should accept and issue such press work. It is extremely unfortunate that the excellent work of the author should be sent out in so unworthy a dress.—C. R. B.

NOTES FOR STUDENTS.

G. K. LEMMON describes in an out of the way place[6] a new lily, *Lilium Kelleyanum*, found near King's river, California, of which we make note that it may not escape attention.—C. R. B.

[4] DALLA TORRE, C. G., and HARMS, H., Genera Siphonogamarum ad systema Englerianum conscripta. Fasc. 5. pp. 321–400. Leipzig: Wilhelm Engelmann, 1903. *M.* 4.

[5] MILLSPAUGH, C. F., Plantae Yucatanae: plants of the insular, coastal and plain regions of the Peninsula of Yucatan, Mexico. Field Columbian Museum, Bot. Ser. 3: 1–84. Illustrated. 1903.

[6] Sierra Club Bulletin 4: 9. 1903.

KARL RUDOLPH has investigated the development of the spines of *Opuntia missouriensis*[7] and finds them purely epidermal and axillary outgrowths, not at all homologous with leaves or branches.—C. R. B.

LUTZ, after experimenting with certain fungi, suggests[8] that alkaloids in plants may be utilizable as plastic material when there is present an adequate supply of nitrates. So also a plant needs carbohydrates in excess before it can utilize asparagin. Lutz directs attention to the fact that certain plants (*e. g.*, aconite and belladonna) are rich in alkaloids when they grow in poor soil, but poor in alkaloids when cultivated in gardens, or when found in a soil rich in nitrates.—C. R. B.

MESSRS. SEWARD AND ARBER have critically examined a number of palm seeds from the Lower Tertiary of Belgium, England, France, and Italy.[9] The conclusion is reached, that they all belong to a single extinct species, *Nipadites Burtini* Brong. It is interesting, that at the present time a monotypic genus, *Nipa fruticans*, prevails in the Sunderbunds and in other southern Asiatic and Malayan deltas. The authors are of the opinion that the presence of *Nipadites Burtini*, together with other tropical forms of vegetation, in the early Tertiary beds of Europe make it extremely probable that a very much warmer climate prevailed at that epoch, than is now found in the same regions.—E. C. JEFFREY.

BENECKE, in an investigation of the formation of oxalic acid in green plants,[10] finds that maize plants form oxalates or not according as he supplies bases for combining with the oxalic acid. If nitrates be supplied, oxalate is produced; if ammonia salts (*e. g.*, sulfate) be used, no oxalate is formed. In other plants (Oplismenus, Fagopyrum, Tradescantia) he only succeeded in modifying the amount of oxalate by the culture conditions. The formation of raphides by Tradescantia was independent of external influences and could only be affected by the supply of calcium. In algae (Vaucheria, Spirogyra) no such relation could be determined. A useful summary of physiological literature of oxalic acid is given.—C. R. B.

HABITUAL POLYEMBRYONY in *Euphorbia dulcis* Jacq. (*purpurata* Thuill.) was described in a preliminary announcement[11] about a year ago. The full paper,[12] with figures, confirms the previous observations. The more extended

[7] RUDOLPH, KARL, Beitrag zur Kenntniss der Stachelbildung bei Cactaceen. Oesterr. Bot. Zeits. **53**: 105–109. *pl. 1.* 1903.

[8] LUTZ, L., Sur le rôle des alcaloids envisagés comme source d'azote pour les végétaux. Bull. Bot. Soc. France **50**: 118–128. 1903.

[9] SEWARD, A. C., and ARBER, E. A. N., Les Nipadites des couches Eocènes de la Belgique. Mém. Musée Roy. d'Hist. Nat. Belgique **2**: —. 1902.

[10] BENECKE, WILHELM, Ueber Oxalsäurebildung in grünen Pflanzen. Bot. Zeit. **61**[1]: 79–110. 1903.

[11] See BOT. GAZ. **34**: 153. 1902.

[12] HEGELMAIER, F., Zur Kenntniss der Polyembryonie von *Euphorbia dulcis* Jacq. (*purpurata* Thuill.). Ber. Deutsch. Bot. Gesell. **21**: 6–19. *pl. 2.* 1903.

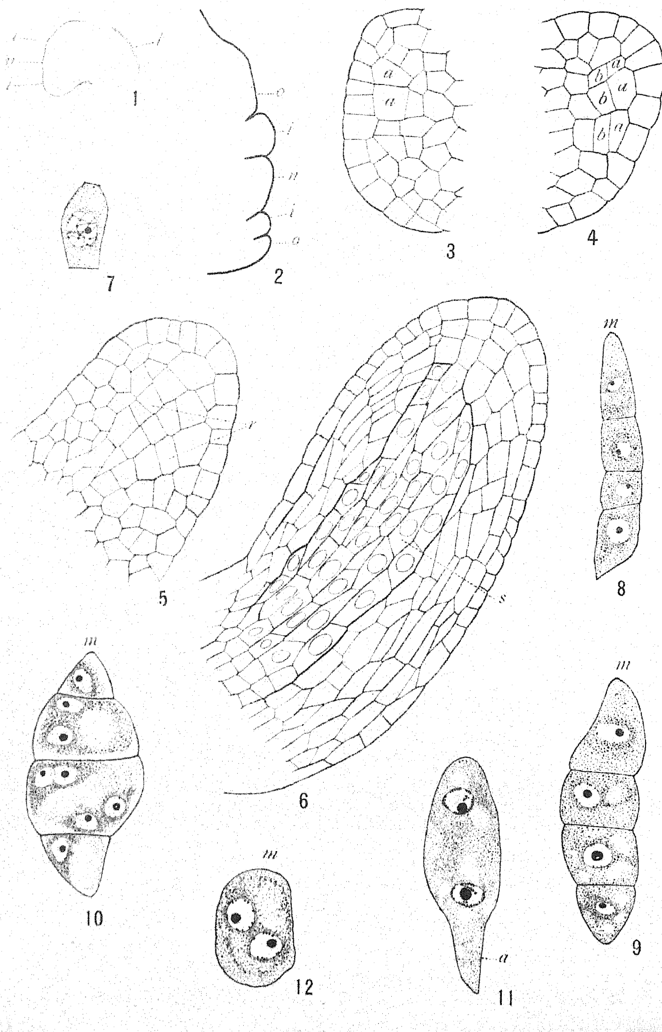
investigations show that about three-fourths of the ovules contain more than one embryo. A considerable percentage of the pollen is sterile and fertilization was not actually observed, although it probably occurs in many cases. Pollination is not necessary for the production of adventitious embryos, at least not for those coming from the nucellus. Whether an embryo would develop from an egg of Euphorbia without fertilization was not determined. Professor Hegelmaier withdraws his earlier statement that polyembryony, as found in Euphorbia, might lead to apogamy.—CHARLES J. CHAMBERLAIN.

IRREGULAR MITOSES in pollen mother-cells and the consequent formation of imperfect pollen have already been noted in several sterile hybrids. In *Cytisus Adami*[13] a hybrid between *Cytisus Laburnum* L. and *C. purpureus* Scop., the development of the pollen is regular, but abnormalities which result in sterility are found in the ovule. After the integuments are quite well developed, a region at the base of the nucellus, rich in protoplasm, begins to grow with great rapidity, so that the nucellus is soon forced out through the micropyle. Often no megaspore mother-cell can be detected; sometimes a larger cell with shrunken protoplasm and a few nuclei indicates that a mother-cell had begun to germinate, and occasionally when the nucellar growth is not particularly extensive, a normal embryo sac may appear. In both the parents the development of the embryo sac is regular.—CHARLES J. CHAMBERLAIN.

ZACHARIAS has published another paper[14] on the chemistry and structure of the nucleus. The present contribution deals with the contents of the nucleus, exclusive of the nucleus and nuclein-containing structures. Pollen mother-cells of Larix, Iris, Hemerocallis, and other forms were investigated. Material was examined in the living condition and also after treatment with various reagents, but sections do not seem to have been used. In dealing with nuclei in division after the nuclear membrane has broken down, the special term, nuclear cavity (*Kernraum*), is used, because the sphere of influence of the nucleus may not be the same as when the nuclear membrane is still intact. The writer believes that Němec's statement that the spindle fibers consist of plastin is too general. Plastin may be present in some cases, while in others it will be lacking. In the living cell during nuclear division the nuclear cavity, with the exception of the chromosomes, appears as if filled with a homogeneous fluid, in which movable thread-like structures may appear between the separating groups of chromosomes. Zacharias believes that his own investigations, as well as those of morphologists, show that definite spindle fibers have not yet been demonstrated in the living cell, and that it is possible that the structures seen in fixed material may be artifacts.—CHARLES J. CHAMBERLAIN.

[13] TISCHLER, G., Ueber eine merkwürdige Wachsthumserscheinung in den Samenanlagen von *Cytisus Adami* Poir. Ber. Deutsch. Bot. Gesell. **21**: 82–89. *pl. 5.* 1903.

[14] ZACHARIAS, E., Ueber die "achromatischen" Bestandtheile des zellkerns. Ber. Deutsch. Bot. Gesell. **20**: 298–320. *pl. 16.* 1902.



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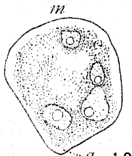

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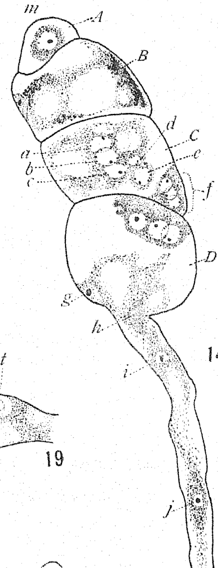

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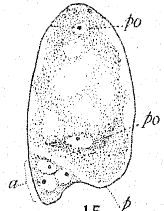

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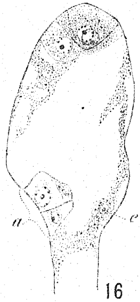

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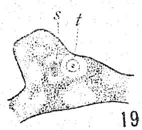

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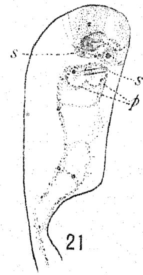

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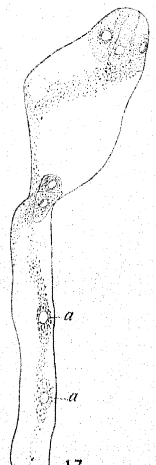

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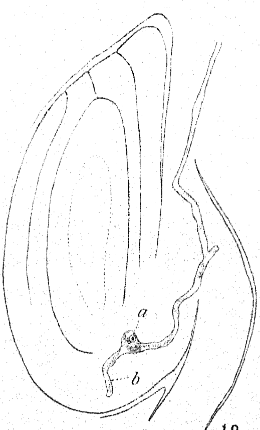

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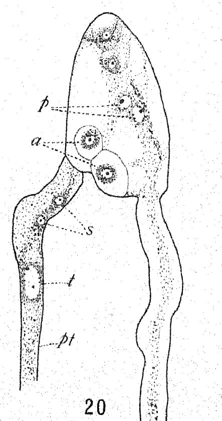

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ASTRUC has brought to a conclusion his work on the acidity of plants.[15] He finds that in non-succulents vegetable acids are made chiefly in the young parts; that is, in the particular regions of cellular activity, of maximum turgescence, and of oxidation. These acids are neutralized or etherized little by little, as has already been shown by other observers. These facts serve to explain the distribution of relative acidity in plants, which gradually diminishes as the development of the organs advances. In succulents, on the contrary, the acidity depends upon slight changes in the external conditions, and these make comparisons sometimes difficult. Thus, the free acids in the Crassulaceae present within a single day enormous variation both in formation and in distribution, so that it is quite impossible to lay down any absolute rule for the occurrence of acids in different leaves of even the same plant. From a great number of experiments, however, Astruc has concluded that the formation of greater or less amounts of malic acid during the night depends on photosynthesis during the day, and is intimately related to respiration and to the greater or less value of the internal respiratory ratio during the night. Incidentally he notes a somewhat remarkable fact, that oxygen is not fixed by the cell when the protoplasm is anesthetized by ether or by chloroform. During the day malic acid diminishes in amount under the influence of respiration and photosynthesis, but if the normal conditions for the plant are changed, that is, if there intervene external causes capable of influencing cell activity, these causes will also influence acidity. Thus sectioning of leaves or changing the constituents of the atmosphere enveloping the plant will induce notable changes in the processes of acid formation or destruction.—C. R. B.

THE DEVELOPMENT of the sexual organs and fertilization in *Picea excelsa* are described in a recent article by Miyake.[16] The pollen grain at the time of shedding, about the second week in May, contains two disorganized prothallial cells, a stalk cell, body cell, and tube cell. The tube begins to form a few days after pollination, and the body cell at once passes into it and divides, giving rise to two male nuclei. At this division the beginning of a cell plate appears at the equator of the spindle, but it soon disappears and no wall is formed; consequently the two male nuclei lie free in a common mass of cytoplasm, and there is no formation of two cells, as described by Strasburger, Belajeff, Dixon, and Coulter. The pollen tube does not branch.

The development of the archegonium is very much as in Pinus. In the neck of the archegonium there are 4–8 cells with 2–4 cells in a row. There are usually four archegonia to each ovule, but the number varies from two to seven. During the growth of the egg no passage of nuclear material from

[15] ASTRUC, M. A., Recherches sur l'acidité végétale. Ann. Sci. Nat. Bot. VIII, 17:109. 1903.

[16] MIYAKE, K., On the development of the sexual organs and fertilization in *Picea excelsa*. Ann. Bot. 17:351–372. *pls. 16–17.* 1903.

the jacket cells into the egg could be detected. The ventral canal cell is formed about a week before fertilization, which, in the neighborhood of Ithaca, occurs about the middle of June. No walls are formed in the proembryo until it has reached the eight-celled stage. Strasburger described walls at the four-celled stage, and other writers have described walls at the four-celled stage in Pinus.

The antheridial cell of Strasburger (third prothallial cell of Belajeff) is called the central cell by Miyake, who regards it as the equivalent of the central cell in the antheridium of pteridophytes. The body cell of Strasburger is called the generative cell. Strasburger refers to the two male cells as generative cells. The terminology is confusing and we are not sure that the present writer has been entirely consistent.—CHARLES J. CHAMBERLAIN.

PLANT HYBRIDS have received but little attention from cytologists. It is known that various species of a genus usually have the same number of chromosomes and that the pollen of sterile hybrids usually have imperfect pollen. Rosenberg[17] has been fortunate in finding a hybrid between parents which differ from each other both in the number and size of their chromosomes. This hybrid is *Drosera rotundifolia* × *longifolia*. *D. rotundifolia* has twenty chromosomes in the sporophyte, this number appearing in the stem, leaf, and root. The chromosomes are short and easy to count. In the pollen mother-cell the number is always ten. In *D. longifolia* the vegetative tissues show forty chromosomes and the pollen mother-cells twenty, just double the numbers in the other species. The chromosomes are also distinguished by being somewhat smaller than in *D. rotundifolia.*

The hybrid is easily recognized by external characters, but is also distinguished by its chromosomes. The mitoses are not different from those of the parents except in the number of chromosomes and the consequent variation in the shape of the spindle. In the sporophyte thirty chromosomes, the sum of the gametophyte numbers of the two parents, was counted in the root, stem, and leaf. In a few cases forty chromosomes appeared in the tapetal cells. In the pollen mother-cells fifteen chromosomes is the dominant number, but twenty often occur, and occasionally mother-cells with ten are found. All three numbers have been found in the same anther. The megaspore mother-cell was not investigated.

The relative number of chromosomes in the parents and hybrid support the theory that the chromosome is a permanent organ of the cell. The fact that three kinds of pollen grains are formed has its bearing upon Mendelism. Professor Rosenberg will continue these investigations.—CHARLES J. CHAMBERLAIN.

IN THE FIRST of a series of studies on the anatomy of ferns, entitled "La masse libéroligneuse élémentaire des Filicinées actuelles et ses princi-

[17] ROSENBERG, O., Das Verhalten der Chromosomen in einer hybriden Pflanze. Ber. Deutsch. Bot. Gesell. 21: 110–119. *pl.* 7. 1903.

paux modes d'agencement dans la fronde," Bertrand and Cornaille[18] describe and discuss, from the taxonomic and anatomical standpoint, the constitution and arrangement of the fibrovascular strands in the leaves of various living orders of ferns. They point out that the petiolar bundle-system of ferns is composed of various combinations of units which they denominate "divergents." Each divergent consists of a protoxylem group placed anteriorly, *i. e.*, toward the upper surface of the frond, and two wings of metaxylem growing out of this posteriorly, *i. e.*, toward the lower surface of the frond. The wood so constituted is typically covered, both dorsally and ventrally, by layers of phloem. The petiolar bundle-systems of the various groups of living ferns may either be gamodivergent, consisting of a number of divergents more or less completely fused together, or dialydivergent, where the divergents are more or less completely separated from each other. In addition the bundle-system as a whole may present various degrees of complexity in the curvatures presented by a line drawn so as to connect all the bundles in a given petiole, etc. The authors point out that there are two striking differences between the petiolar fibrovascular system of the ferns (or Megaphyllides as they term them) and that of the cycads; for in the latter the fibrovascular units corresponding to the divergents, instead of having two wings as in the ferns, are monopolar, and further the protoxylem, instead of being placed anteriorly and toward the upper surface of the leaf is posterior and next the lower surface of the frond, being thus centripetal as in the lycopods. The authors are of the opinion that there should, as a consequence of these differences, be a good deal of reserve in the matter of deriving the cycads from a filicineous stock, as is the almost universal tendency at the present time.— E. C. JEFFREY.

THE formation of the spores in *Rhizopus nigricans* and *Phycomyces nitens* is described by Swingle in a recent *Bulletin*[19] of the Bureau of Plant Industry. Pure cultures were obtained, the material was fixed, sectioned, and stained, according to the most approved cytological methods. The paper deals especially with the mechanics of the peculiar cell division found in these sporangia, and with the nature and functions of the vacuole. It is of interest to note that the four genera of the Mucorineae which have now been carefully investigated, Pilobolus and Sporodinia studied by Harper, and Rhizopus and Phycomyces studied by the present writer, differ considerably in the formation of their spores. The following is Swingle's own summary of the process:

[18] BERTRAND, C. E., and CORNAILLE, F., Étude de quelques caractéristiques de la structure des Filicinées actuelles. Travaux et Mémoires de l'Université de Lille 10: —. 1902.

[19] SWINGLE, DEANE B., The formation of spores in the sporangia of *Rhizopus nigricans* and *Phycomyces nitens*. U. S. Dept. of Agric., Bureau of Plant Industry. Bull. 57. pp. 40, *pls. 6.* 1903.

1. Streaming of the cytoplasm, nuclei, and vacuoles up the sporangiophore and out toward the periphery, forming a dense layer next the sporangium wall and a less dense region in the interior, both containing nuclei.

2. Formation of a layer of comparatively large, round vacuoles in the denser plasm, parallel to its inner surface.

3. Extension of these vacuoles by flattening, so that they fuse to form a curved cleft in the denser plasm; and, in the case of Rhizopus, the cutting upward of a circular surface furrow from the base of the sporangium to meet the cleft formed by these vacuoles, thus cleaving out the columella.

4. Division of the spore-plasm into spores; in Rhizopus, by furrows pushing progressively inward from the surface and outward from the columella cleft, both systems branching, curving, and intersecting to form multinucleated bits of protoplasm, surrounded only by plasma-membranes and separated by spaces filled with cell sap only; in Phycomyces, by angles forming in certain vacuoles containing a stainable substance and continuing outward into the spore-plasm as furrows, aided by other furrows from the columella cleft and dividing the protoplasm into bits homologous with and similar to those in Rhizopus, and separated by furrows partly filled with the contents of the vacuoles that assist in the cleavage.

5. Formation of walls about the spores and columella, and, in the case of Rhizopus, the secretion of an intersporal slime.

6. Partial disintregration of the nuclei in the columella.—CHARLES J. CHAMBERLAIN.

AN EXCELLENT ACCOUNT of the sexual processes in *Plasmopara alpina* Johans. by Rosenberg[20] adds another form to the list of Phycomycetes which are now receiving so much attention.

Plasmopara conforms in all essentials to the condition in Peronospora and Albugo. The oogonium contains at first about forty-five nuclei, which number is doubled by the first mitosis. All of these pass into the periplasm excepting one, which remains in the ooplasm near a coenocentrum. There is then a second mitosis, affecting almost all of the nuclei. The nucleus in the ooplasm divides, forming the female nucleus, which remains close to the coenocentrum, and a sister nucleus that passes to one side and breaks down. Thus proximity to the favorable conditions around the coenocentrum determines the selection of the functional gamete nucleus here as in others of the Peronosporales and in the Saprolegniales.

The antheridium contains at first about five nuclei, which are increased to ten or twelve by mitosis. One male nucleus is introduced into the egg and fuses with the female.

Of especial interest are Rosenberg's views on the significance of the mitosis in the oogonium and antheridium. The author considers these as

[20] ROSENBERG, O., Ueber die Befruchtung von *Plasmopara alpina*. Bih. Svensk. Vet.-Akad. Handl. 28:—. [1–20. *pls. 2.*] 1903.

comparable to the tetrad divisions in higher plants, meaning the two mitoses in the spore mother-cell. The nucleus passes through a synapsis condition before the first mitosis. The spindle is intranuclear with small granular bodies at the poles as in others of the Peronosporales. In the second mitosis the spindle is less distinct, as Stevens noted in Albugo. The number of chromosomes appears to be about the same in each mitosis. Rosenberg regards the synapsis as indicating a reduction of the chromosomes, in agreement with the generally accepted history of the spore mother-cell, and considers its presence in relation to the two mitoses as establishing analogies with these events.

The reviewer has recently discussed the behavior of the nucleus during gametogenesis in the Phycomycetes[21] and regrets that he could not have included Rosenberg's views in that account. However, his opinions are not changed by these results. It is not established that synapsis has any relation to reduction phenomena in the thallophytes, and it is also being reported among higher plants in tissues where there is no reduction. The number of mitoses in the gametangia of Phycomycetes is quite variable. There is only one in the oogonium of Saprolegnia and in certain species of Peronospora and Pythium. This mitosis is probably a phylogenetic reminiscence of times when many gametes were formed in these gametangia. A second mitosis is probably merely a continuation of the tendency to multiply the nuclei and would be carried farther if nutritive conditions allowed. The second mitosis is more likely to be found in the ooplasm, because that portion of the cell is unquestionably better nourished, which explains its entire or partial absence in the periplasm. There is excellent evidence that the second mitosis is weaker in kinoplasmic material than the first, thus showing the effect of unfavorable conditions in the cell.

This is not saying that reduction phenomena may not take place just previous to the mitoses in the gametangia of Phycomycetes, but comparisons between these mitoses and the events in the spore mother-cell are not likely to have much value in establishing the supposition. To the reviewer the probabilities seem all against the existence of reduction phenomena previous to gametogenesis in plants, for it is more natural to expect it either immediately after the sexual act or at the end of a sporophyte generation. The proof must come through studies of the nucleus at various periods of ontogeny and the evidence will accumulate slowly. We do not know of any better forms for such investigations than some of the Peronosporales, unless they be certain Chlorophyceae which have not received their fair share of attention in the cell studies of recent years.—B. M. DAVIS.

ROTHERT has studied the effects of ether and chloroform on the sensibility of microorganisms.[22] Knowing that narcotics affect the various functions of

[21] DAVIS, B. M., Oogenesis in Saprolegnia. BOT. GAZ. 35:339–342. 1903.

[22] ROTHERT, W., Ueber die Wirkung des Aethers und Chloroforms auf die Reizbewegungen der Mikroorganismen. Jahrb. Wiss. Bot. 39:1–70. 1903. The title is

higher animals differently according to the concentration and duration of action, so that the effects can be arranged in a graded series, he proposed to himself the solution of the question whether a similar gradation in narcosis existed among plants and the protozoa, in which the differentiation and division of labor has not gone so far. If, for example, their sensitiveness to external stimuli could be suspended more easily than other vital phenomena, it would be possible by partial narcosis to make them insensitive (*i. e.*, to produce anesthesia), without at the same time suppressing those functions (growth, movement, etc.) by means of which a visible reaction could be executed. Thus an important means of analyzing irritable reactions might be secured.

After securing suitable material (a matter of great difficulty), tests were made (1) by putting organisms into vials containing water with known percentages of the narcotic, with precautions against its evaporation; (2) by using mounted preparations, the cover being supported, in which were introduced Pfeffer's capillary tubes (for chemotaxis) or air bubbles (for aerotaxis); or (3) by means of hanging drop cultures in a moist chamber. The criterion for the existence of sensibility was the accumulation of the individuals in definite regions.

Naturally, though not the chief aim, many observations were made on the effect of narcotics on motility. The resistance of nearly related organisms is very different; *e. g.*, one form of *Bacterium termo* ceased to move in 20 per cent. ether-water,[23] while many individuals of another form, apparently the same species, resisted a saturated solution of ether for five hours. Similarly *Gonium pectorale* has its movements slowed by 2.5 per cent. ether-water and wholly stopped by 20 per cent.; whereas *Chlamydomonas sp.?* moved normally in 20 per cent. ether-water and was only stopped by 60 per cent. Individual differences are also noticeable.

Rothert found various forms in which the osmotactic, chemotactic, aerotactic, or phototactic sensitiveness could be suspended by the narcotics, while movement was not. Thus in one form of *B. termo*, chemotaxis and aerotaxis were only slightly reduced by moderate concentrations, while osmotaxis was completely checked. In *Bacillus Solmsii* chemotactic sensibility was stopped by chloroform but not by ether.

A curious reversal of phototactic reaction occurred with chloroform, both in Chlamydomonas, which cannot be anesthetized, and in Gonium, which is easily made insensible. These organisms, which were reacting negatively,

inappropriate to the paper, for Rothert specifically says (p. 15): "The question as to the influence of narcotics upon the motility of microorganisms I did not consider the object of my investigations." Nor are the researches confined to "microorganisms," as this term is commonly used, though all the forms studied were microscopic.

[23] *I. e.*, a 20 per cent. solution of a saturated solution of ether in water at room temperature; similarly designated in other cases.

immediately upon treatment with weak chloroform-water reacted positively. In other words, the critical intensity of light (*i. e.*, the point at which a given organism will not react) was raised by the chloroform, so that what they fled from before, they now sought. This effect disappears gradually, and the faster the weaker the chloroform. Ether produces no such effect. Immediately after a phototactic organism recovers from a dose of ether or chloroform, its reaction is always negative. If normally positive, the reaction is reversed; if normally negative, the reaction is intensified; *i. e.*, the critical intensity of light is lowered.

The results reached by Rothert regarding the specifically different susceptibility of related forms to narcosis are quite irreconcilable with the statements of Overton, who holds[24] that this susceptibility depends on the grade of differentiation of the cells, as indicated by the rank of the organism. Even individual differences were found by Rothert to be great.

It is found to be characteristic of the anesthetic effect of ether and chloroform on microorganisms that it depends only upon their concentration and not upon the duration of their action. Anesthesia appears instantly and disappears as quickly. No solution which is too weak to effect anesthesia at once will produce it by prolonged action. Some observations indicate that solutions too weak to produce complete anesthesia will diminish the degree of sensitiveness to stimuli. The effect of these narcotics on movement, however, is quite different; for this depends both on their concentration and the duration of their action.

This paper adds valuable data to our present knowledge of the narcosis in plants, for which previously we have been chiefly indebted to Overton.—C. R. B.

[24] Studien über die Narkose. Jena. 1901.

OPEN LETTERS.

Flora of St. Croix.

I HAVE, quite by chance, just come across *The flora of the island of St. Croix*, published by C. F. Millspaugh in the Feld Columbian Museum Bot. Series, Vol. I, no. 7, which was issued at the end of last year. In Mr. Millspaugh's work no notice whatever is taken of the species published by Mr. Paulsen and the writer in a floristic appendix to our work "Om Vegetationen paa de dansk-vestindiske Öer;" though Mr. Millspaugh in his introduction gives a complete translation of the lines from Urban's "Bibliographia" dealing with our work: "In a floristic appendix six phanerogams new to the Danish islands and Rostrup's fungi and lichens are listed."

We are thus led to believe that the author has not taken the trouble to read our paper.[1] Nor has he apparently made himself acquainted with the additions to Urban's "Bibliographia," which occur in later numbers of the *Symbolae Antillanae*. The result is that none of the species of phanerogams, fungi, and lichens published by us have been included. The author also gives a short list of algae, containing, according to his typography, species new to the island. But hardly any of them are really new, as almost all of them, and several others, are mentioned in my short paper, "A contribution to the knowledge of the marine algal vegetation of the coasts of the Danish West-Indian islands." I have, moreover, distributed some St. Croix algae in Wittrock and Nordstedt's exsiccatae, and in Phycotheca Amer.-bor.

It is of course of great interest to have the new finds in St. Croix published, but this could have been done as an appendix to the flora of the islands. But when Mr. Millspaugh sets out to give a complete list, we are justified in expecting that everything published regarding the flora of the islands will be included.—F. BÖRGESEN.

IT IS distinctly stated on page 459 of the publication referred to that it *only* includes the work of the Rickseckers, checked by the only published general list of the island flora, viz., Eggers's. It was not the intention to include scattered lists. All of Urban's publications which were available up to the date of sending in copy were made use of.—C. F. MILLSPAUGH.

[1] Bot. Tidskrift, 1898, and Revue Gén. Bot., 1900.

NEWS.

DR. B. E. LIVINGSTON has been granted a research scholarship by the New York Botanical Garden, where he will spend some months on leave of absence from the University of Chicago.

HOMER R. FOSTER, for the past five years professor of botany in the University of Washington, has resigned to take up commercial work in connection with a large hardwood lumber firm in Chicago.

CHARLES J. BRAND, who for the past year has been assistant in plant economics at the Field Columbian Museum of Chicago, has been promoted to the position of assistant curator, department of botany, in that institution. Mr. Brand is a graduate of the University of Minnesota.

MR. C. G. LLOYD, of Cincinnati, seems to have been elected a member both of the German Botanical Society and of the Botanical Society of France. Though the Germans print the name L. G. and the French C. J., it is doubtless our well-known mycologist who is intended in both instances.

THE FRENCH NATIONAL SOCIETY of Agriculture has awarded a gold medal to M. Lucien Daniel for his researches on grafting; a silver medal to M. Paul Parmentier for his *Traité de botanique agricole;* and a bronze medal to M. Th. Husnot (best known as a bryologist) for a book on *Les pres et les herbages.*

THE BOTANICAL GARDEN of Buitenzorg has begun issuing still another publication, entitled *Icones Bogonienses*, in which are to be described and figured new or little-known species of the Dutch possessions, or species cultivated in the garden. Four fascicles have already appeared, and others are to be published at irregular intervals.

THE HERBARIUM of the late Alexis Jordan has been acquired by the Catholic University of Lyons. The duplicates are to be sold, at prices varying from 20 fr. to 12 fr. per 100, according to the completeness and quality of the sets. The best will contain from 7,000 to 12,000 species. Applications may be made to Professor Roux, rue du Plat, Lyons, France.

EDMUND P. SHELDON and M. W. Gorman have undertaken a botanical expedition to the "Three Sisters," snow peaks of the Cascade range in Oregon. These mountains, unnamed and for the most part unknown, are all over 10,000 feet high, and the obsidian cliffs, glaciers, and waterfalls of the region are said to be wonderful. It is likely that the trip will yield a large number of interesting plants.

THE VERMONT BOTANICAL CLUB held its ninth annual field meeting at Arlington and Manchester in southern Vermont on July 3 and 4. There was a good attendance, including visiting botanists from Minnesota, New York, Massachusetts, and New Hampshire. The weather was ideal and the ascent of Mt. Equinox, under the guidance of Judge and Mrs. Loveland Munson, was a delightful mountain climb which afforded much of botanical interest. This club now has about one hundred and sixty active members.

DR. H. G. TIMBERLAKE, assistant professor of botany in the University of Wisconsin, died suddenly on July 19 at the age of thirty. He was taking a bath and seems to have slipped on the curved bottom of the enameled tub and fallen over the side, striking his head violently on the floor and rupturing a cerebral artery. Death occurred before a physician could reach him. Dr. Timberlake had recently been promoted to an assistant professorship and was married on June 30 to Miss Violet Slack, an assistant in the department.

THE COMMITTEE OF ORGANIZATION for the International Botanical Congress at Vienna plans to have the meetings on June 13-18, 1905, giving the mornings to addresses and discussions of topics of present importance (a morning to some one subject), and the afternoons to the nomenclature problem. The morning of the fifteenth will be reserved for a meeting of the Association internationale des botanistes. A great botanical exposition is planned, at the time of the Congress, in the palace at Schönbrunn; and excursions, botanic and scenic, before and after the Congress, will be arranged.

IT IS PROPOSED to organize a society for horticultural science, the object of which shall be more fully to establish horticulture on a scientific basis. The membership will naturally be made up of the horticulturists of the experiment stations and of the U. S. Department of Agriculture, together with other scientific men whose work has a horticultural bearing. The meetings will be held in connection with those of some kindred society, as the American Pomological Society or the American Association for the Advancement of Science. Any botanists interested are requested to address S. A. Beach, Horticulturist, New York Agricultural Experiment Station.

WITH THE TENTH VOLUME the *Annuario del Real Istituto Botanico di Roma*, founded by Professor R. Pirotta in 1884, comes to an end. In its place there is to appear the *Annali di Botanica*, which will be published in small fascicles in order to avoid the long delay of a more voluminous journal. The new publication will include not only original researches in all fields of botany, but also analytical reviews of important papers and synthetical reviews of current questions. Particular attention will be given to the history of botany in Italy and to making known all facts regarding the Italian flora. The first fascicle was published on May 15, and the second on June 30.

VOLUME XXXVI NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER, 1903

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.[1]

W. F. GANONG.

(WITH SIXTEEN FIGURES AND MAPS)

AT the head of the Bay of Fundy, in the Provinces of New Brunswick and Nova Scotia, occur extensive and diversified salt marshes. In places they merge into fresh-water bogs; elsewhere, and for most of their area, they are reclaimed from the sea and in a high state of cultivation, or are in process of reclamation; and some parts remain still in their natural state. Corresponding with these marked differences of conditions are striking differences in the vegetation; and the constant operations of diking, flooding, etc., allow all gradations of conditions, and hence of vegetation, to be seen. There is here offered, therefore, an unusually favorable opportunity to investigate some phases of the dynamical relations of plants to their environment, particularly the effects of soil and water upon their forms and sizes, upon the determination of the kinds that occur in such places, and upon the succession of one kind by another. In the present paper are contained the results of the observations I have

[1] No. 1. Upon raised peat-bogs in the Province of New Brunswick. Trans. Roy. Soc. Canada II. 3^4: 131–163. 1897.

No. 2. A preliminary synopsis of the grouping of the vegetation (phytogeography) of the Province of New Brunswick. Bull. Nat. Hist. Soc. New Bruns. 5:47–60. 1903.

The present paper was presented in abstract before the Society for Plant Morphology and Physiology at the Yale meeting, December 28, 1899.

been able to make upon these subjects during some eight weeks of field work in the summers of 1898, 1899, and 1901, together with such a summary of the origin and development of the marshes as seems necessary to an understanding of the present subject.

Literature and other sources of information.

From the present, or indeed, from any, point of view, there is practically no scientific literature upon the vegetation of these marshes. A very brief list, of but six species, of the plants characteristic of the wild salt marsh was given by Goodwin in 1893, and references to a species or two occur in some of the papers later to be cited; but further there is nothing. Upon the geological origin, structure and economics of the marshes, however, there are valuable publications to be mentioned later. As to the literature of salt marshes in other parts of America, this also is scanty. Shaler, in two or three of his works, has given brief descriptions of the mode of formation and economics of those of the Atlantic coast of the United States, and, recently, valuable contributions have appeared by Kearney, by Harshberger, and by Lloyd and Tracy. There are references to salt marshes in Warming's and in Schimper's well-known general works, and there are papers on the salt marshes of Europe by Warming, by Flahault and Combres, and by others, and there is a synopsis of those of Germany in Drude's work.

Any account of the changes in vegetation brought about in the process of reclamation of the sea-bottoms in the Netherlands would be of interest in this connection, but such I have not found, nor have I been able to see a paper by Theen on the diked marshes of Schleswig-Holstein, mentioned by Drude (p. 390). Upon bogs, into which the marshes often merge, there is of course an ample literature, partly summarized in the first paper of this series. All of the works above-mentioned will be referred to their proper places later, and are cited in full in the bibliography at the end of this paper.[2]

[2] In the marsh country there are residents who are experts in all matters pertaining to the economics of the marshes, and from several of them I have obtained most valuable information, which I wish here gratefully to acknowledge. I am particularly indebted in this way to Mr. W. C. Milner, of Sackville, President of the Misse-

The distribution and extent of the marshes.

The marshes now under discussion possess, as will later be shown, peculiarities which clearly differentiate them from the ordinary salt marshes so common everywhere about the mouths of tidal rivers in this country and in Europe, and hence are of a type rare if not unique. The ordinary marshes are also abundant in this region (though of small extent), particularly along the Gulf of St. Lawrence shore. Others, more like those we are considering, occur in the Bay of Fundy at Annapolis Basin, at Musquash, at Pisarinco, at St. John, at St. Martins, at Martins Head and elsewhere, sometimes diked and sometimes not. But in their complete and perfect form, the Fundy salt marshes are confined to the two heads of the Bay, *i. e.*, to Minas Basin and Chignecto Bay; and they are largest and finest in the latter. Their extent and distribution are very clearly shown upon the surface geology maps of this region, and, for Chignecto Bay, in the accompanying map (*fig. 1*). In Chignecto Bay they begin at Rougie (or Petit Rocher), just west of Cape Enrage, and thence extend irrregularly to the Shepody River; they occur in places along the Petitcodiac and Memramcook Rivers, and reach their perfection of size, economic value and scientific interest at the head of Cumberland Basin, whence they radiate up the valleys of the several small rivers of that district, the Tantramar, Aulac, Misseguash, LaPlanche, and (to a lesser extent) the Nappan, Maccan and Hebert. Largest of all is the combined Tantramar-Aulac marsh, shown in detail upon the accompanying map (*fig. 2*), and it is this, with the Misseguash marsh and the Shepody marsh, that I have studied.

The total area of the marshes with the related bogs is only approximately known. In 1895, Mr. Chalmers, of the Geological Survey, after a careful computation, estimated 34,300 acres of diked and undiked marsh in New Brunswick, of which 9,100 acres were in Albert county west of the Petitcodiac, and 25,200 in Westmorland north of the Misseguash. Mr. Monro, a profes-

guash Marsh Co.; to Mr. Howard Trueman, of Point de Bute; and to Mr. William Fawcett, of Upper Sackville. Mr. F. A. Dixon, of Sackville, has aided greatly by collecting for me seeds of many of the marsh plants.

sional surveyor who was engaged upon all of the principal surveys of these marshes, estimated in 1883 that the diked marsh (the undiked is comparatively insignificant in quantity) on the Nova Scotia side of the boundary contained 12,600 acres, while New Brunswick had on the Tantramar, Aulac and Misseguash,

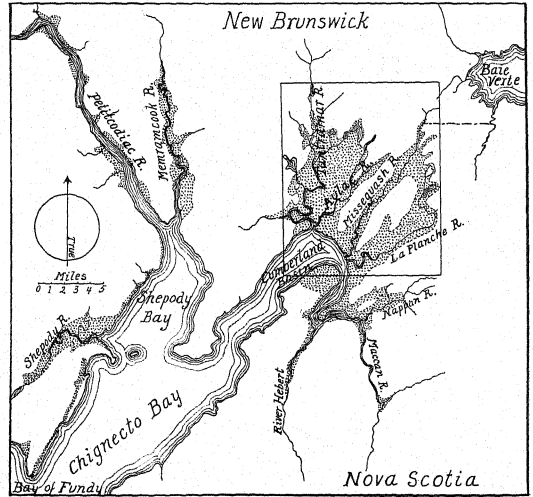


FIG. 1.—Sketch map of the marsh country, showing (dotted) the distribution of the principal marshes. The area enclosed by the quadrangle is shown enlarged in *fig. 2*.

19,400 acres. Of still unreclaimed bog lands (everywhere underlaid by marsh), there were on the LaPlanche 1,000 acres, on the Misseguash 3,700 acres, and on the Aulac and Tantramar 4,000 acres. Thus there are about 40,700 acres of marsh and bog about Cumberland Basin, of which 25,000 acres belong to New Brunswick, and 15,700 acres to Nova Scotia. Their approximate extent in this vicinity, and the relative amounts of wild

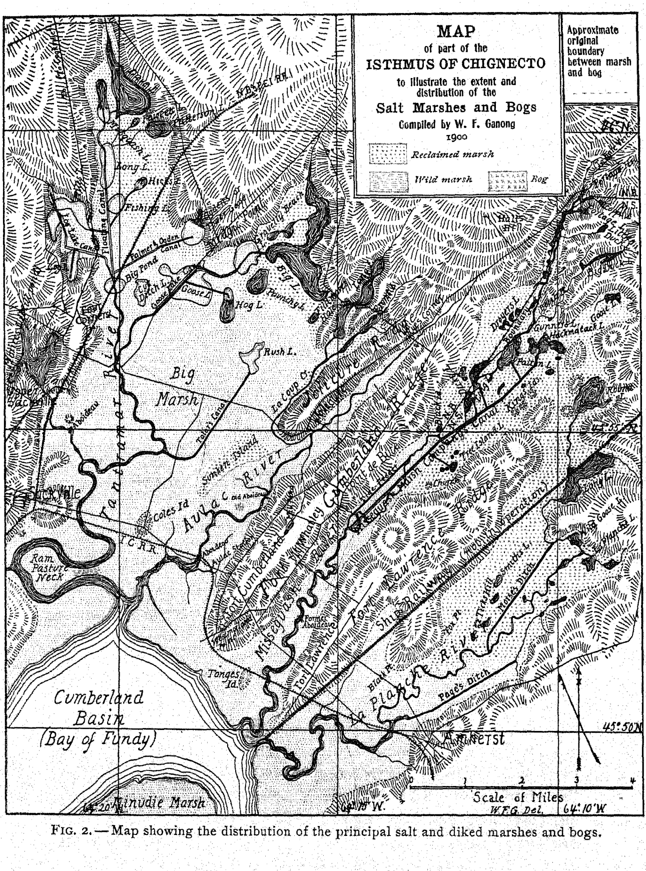
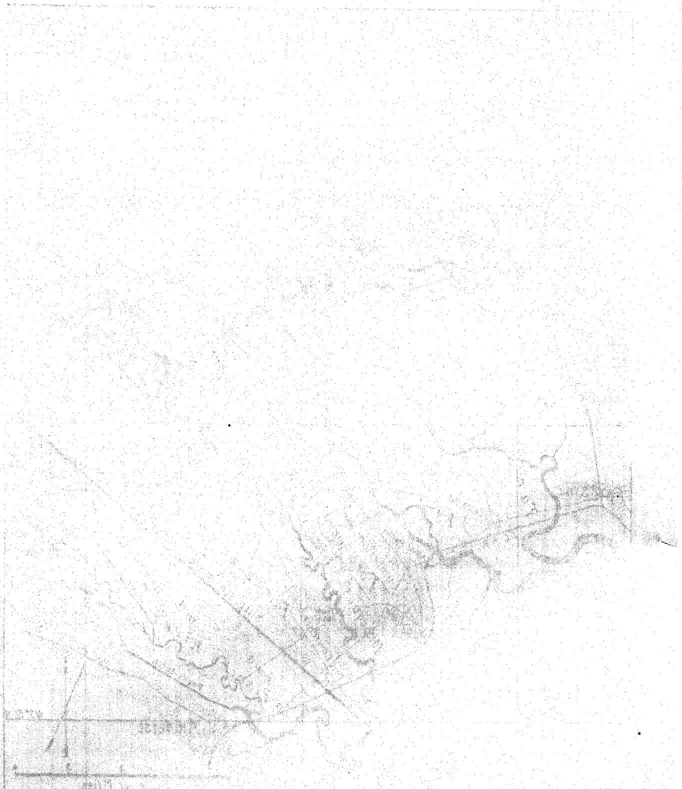


FIG. 2. — Map showing the distribution of the principal salt and diked marshes and bogs.



and reclaimed marsh and bog, together with the outlines of these marshes, may be gathered from the accompanying map (*fig. 2*) drawn to the scale of two miles to an inch. The marshes on Minas Basin are much less in area than those on Cumberland Basin, but in the aggregate there are at the head of the Bay of Fundy not far from 70,000 (or as Hamilton estimates, 80,000) acres of marshes and bogs, of which by far the greater part is diked and under cultivation. The extent of the diked marshes may be yet better understood when it is stated that, according to Shaler, the entire area of all of the diked salt marshes of the eastern United States does not exceed 5,000 acres.

The characteristics of the marsh country.

The country around Cumberland Basin is of ancient (Palaeozoic) formations, rounded into low smooth hills and ridges separated by radiating river valleys. Among the ridges lie the marshes, seemingly level as the sea; and, like it, they fill bays, surround islands and are pierced by points. Seen from the neighboring ridges, the marshes have an aspect characteristic and beautiful. They are treeless, but are clothed nearly everywhere with dense rich grasses in many shades of green and brown, varying with the season, with the light, and even with the winds. For the most part the merging of the colors is irregular; but in places, owing to the different treatment given by different owners to their land, or to the presence of fields of grain or pasture-lots, there is something of the checkered appearance usual in highly cultivated land. The frequent ditches marked by denser growths, the rare fences and the occasional roads or railways are other signs of the operations of man. Towards the sea are narrow fringes of unreclaimed marsh, poorer in vegetation and generally duller in color, while farther back the green of the marshes gives place to the brown and gray of the bogs, which are further distinguished by irregular shrubbery and trees, and many little lakes. Nobody lives upon the marshes, but scattered upon them are many great barns, all of one and the simplest pattern, unpainted and gray from the weather, standing at any and every angle. These barns are one of the distinguishing features of the marshes, and give to

them a suggestion of plenty which is a true index of the economic condition of this region, for here are the most prosperous and progressive farmers, and the most thriving country towns in eastern Canada. Especially characteristic of the marshes are the tidal rivers which have helped to build them. As is well known, the sea here shows a great range of tides, even to over forty feet.[3] The tidal rivers, winding in the most sinuous courses through the marshes, at times run full to their bordering dikes, loaded with brownish-red mud; but the fall of the great tides sends their thick currents tumultuously out, to leave but tiny rills between deep gaping gashes of slippery mud gleaming in the sunlight. Thus too are extensive flats laid bare about Cumberland Basin. The suspended mud gives both to the rivers and to the sea a dull-red color which is a striking and a characteristic feature of the scenery of the marsh country. Not all of the rivers, however, are red, for from some of them the sea has been shut out by ingenious dams, and in each of these the banks are clad with dense green grass to near the bottom of the bed, along which winds a small fresh-water stream.

When one goes upon the marshes from the upland, he is likely to think them misnamed; for instead of the soft bottom and the rank growth associated with the word marsh, he finds everywhere a soil as firm as the upland itself, and, on the reclaimed parts, a growth of the finest grasses, luxuriant but not coarse. Indeed, a near view of the reclaimed marsh shows scarcely anything different from the best of fine-soiled upland grass land.

The marsh country is beautiful to look upon, and in addition there hovers over it the charm of a long and varied history. It was a part of the ancient Acadia and inherits the memories of

[3]The height of the tides in this region is popularly exaggerated. Careful measurements have given for Cumberland Basin a range of 38 feet for neap and of 45.5 feet for spring tides. Exceptional tides have had greater range, and the greatest on record (the Saxby tide of 1869) had a range of about 70 feet. The tides at the head of Minas Basin are ordinarily somewhat higher than in Cumberland Basin. Fuller particulars may be found in the Admiralty charts, in a "Report . . . . on the construction of a canal between the Gulf of St. Lawrence and the Bay of Fundy," Ottawa, 1874, and in a Report on a "Survey of tides and currents in Canadian waters," by W. Bell Dawson, Ottawa, 1899.

that picturesque but ill-fated country. The student in his wanderings meets with many a reminder of the ancient régime.

The geological origin of the marshes.

An understanding of the origin and formation of the marshes is so important to the interpretation of some of the peculiarities of their vegetation, that a somewhat full account of it is needful here.

The subject was first touched upon by Lyell (in his *Travels in North America*, 1845), but received its first systematic discussion from Dawson (in his *Acadian Geology*, 1855, repeated in later editions). Subsequent accounts, with some additional facts, are given by Monro (1883), by Chalmers (1895), by Trueman (1899), and in more popular fashion by Dixon (1899); while an extremely good synopsis of the whole subject has been contributed by Eaton (1893). From the point of view of the tidal action in their formation there are papers by Hamilton (1867), by Matthew (1880), and by Murphy (1886), and of course scattered references by others.

The central fact in the formation of the marshes is this: they have been, and still are being, built in a subsiding basin out of inorganic red mud brought in from the sea by the rush of the tides, whose height is the determining factor in their height. Practically no part of their mass has been built from detritus brought down by rivers, which in this region are altogether insignificant in volume; nor has vegetation, either marine or land, helped to any appreciable extent to build them. I believe no observer of the mode of their formation could doubt that they would be as high and wide as they are today had never a plant grown about or upon them. It is these two facts, their formation out of a purely inorganic mud brought in by the sea, and the lack of cooperation of plants in their building, which differentiate them from the salt marshes so common elsewhere about the mouths of tidal rivers.

Whence, then, comes this great store of rich mud? On this all students agree; it is from the red Permo-Carboniferous sandstones forming the sides and bottoms of the channels between the marshes and the Bay of Fundy. These soft rocks are

rapidly eroded by the strong tidal currents, which, in their onward rush to the northeast, carry the detritus whirling in suspension, to drop it as their force is checked by their quiet spread over the marshes at the highest tides. Thus, the sea bottom supplies the materials, the rush of the tidal currents the power to remove, carry and lift them, and the quiet of the waters at the turn of the tide the condition allowing them to be dropped. In this way the sea is building up the land, perhaps on a greater scale here than elsewhere on the globe.[4]

The quantity of mud needed to form the marshes has been immensely great. Not only do they cover many square miles, but borings show that they can be as deep as eighty feet at least;[5] and moreover, the marsh mud extends also everywhere under the bogs and shallow lakes clear to their utmost bounds. To supply this quantity, the channel to the bay (Chignecto Channel) must have been enormously widened and deepened, and hence it must have been very small when the process began. The sea has quarried out the channels, and the marshes are the debris. This process has been aided, or, perhaps more properly, has been allowed, by the recent subsidence of this region, of which the indisputable evidence is found in the buried forests well known to exist at several points under the marsh much below high-tide level. Dawson first described the stumps of a beech and pine forest, the wood still sound, rooted on Fort Lawrence Ridge, thirty to thirty-five feet below high-tide level. Chalmers and others have described other cases, particularly stumps laid bare, over thirty feet under the surface, in the ship-railway dock,[6] and I

[4] The power of these tidal currents in eroding the underlying rocks has been well set forth by Matthew, in his "Tidal erosion in the Bay of Fundy."

[5] Chalmers, Geological Report 1885, M, 129: according to the same investigator however (*op. cit.* 41) this depth appears to be so great in consequence of a fault at this place. He apparently means that the downthrow took place while the mud was accumulating. The depth of 150 feet assigned to the mud at this place by Trueman, is based, as he informs me, upon the recollection of a resident as to the depth of the boring described by Mr. Chalmers. The official figures of the latter, however, make the depth somewhat under 80 feet.

[6] The ship-railway, a great work designed to transport vessels across the Isthmus of Chignecto by rail in lieu of a canal. Though over three-fourths finished, work upon it has been suspended and is unlikely to be resumed.

have myself seen such stumps in position. The soundness of the wood shows how recent the subsidence must have been. Another fact important in this connection is the presence of a bed of peat twenty feet thick under eighty feet of marsh mud, as shown by a boring at Aulac described by Mr. Chalmers. The same observer has also found that in other places the marsh mud is underlaid by post-glacial clay containing shells of species still living in this region, though in clearer and quieter waters than now prevail in Cumberland Basin, and that this clay merges without break into the marsh mud. Grouping together these facts, the history of the marshes would appear to have been as follows. At a comparatively late post-glacial period, the land must have stood much above its present level.[7] At that time the present Cumberland Basin was a shallow lake around which peat bogs were growing; it received the waters of the seven small rivers still flowing into it, and emptied by a single narrow fresh-water channel along the course of the present Cumberland and Chignecto Channels.[8] The subsidence of the land (the same which has drowned the lower valleys of the St. John, St. Croix and other rivers of this region), allowed the tide to creep farther and farther up this channel until it reached the lake above, which it converted into a brackish, and later a salt, lagoon. At first the water would not be very muddy nor the tidal fluctuations great in the lagoon; but as the land continued to sink, the currents would become more powerful, erosion more active, and the water so muddy that marsh formation would begin around the margin of the basin and at the head of tide on the rivers. Thus, gradually, the conditions of the present day were brought about.[9]

[7] Not necessarily over 80 feet, the greatest known depth of the marsh mud, and even much less if Chalmers (Report, 41) is correct in ascribing a part of this depth to post-glacial faulting.

[8] The depth of the channel to the sea is consistent with this view. The best Admiralty chart (No. 354, "River Petitcodiac and Cumberland Basin") gives the least depth over a rock bottom as 5½ fathoms at extreme low tide, or about 80 feet below high tide. A deeper channel may however exist in the mud or sand on either side of the rock bottom.

[9] An important question arises as to whether this subsidence is still in progress. The evidence is conflicting, and the various students of the subject are not agreed. I believe it is still in progress for these reasons: first, it is still going on in other parts of

The mode of formation of the marshes.

So much for the origin of the marshes as a whole; we consider next the actual process of marsh-building by the sea. It may best be observed along the tidal rivers, which play an indispensable part in the building of the greater marshes. At ordinary tides the rivers do not overflow their banks nor reach the dikes at all. But at the spring tides every month they rise higher, the waters rush more swiftly, and, gathering up yet more mud from banks and bed,[10] overflow the banks, and, unless stopped by the dikes, spread abroad over the marshes. When the water thus leaves the channels, however, its speed is at once checked, and soon it comes to entire rest: it can no longer carry its burden of mud, and drops most of it. The water leaves the rivers so muddy one can see scarcely an inch or two into it; it returns, a few minues later, fairly clear. The thickness of mud deposited at a single tide varies from a small fraction of an inch on the higher places, to several inches on the bottoms of lakes which have been opened by canals to the tide.

The powerful tidal currents in the crooked rivers cause constant and rapid changes in the soft muddy banks, and all the phenomena of the wandering of rivers in a flood plain may here be seen upon an unusual scale. In fact the marshes are really the flood plains of the tidal rivers, though built by materials

Acadia (as shown in Bulletin of the Natural History Society of New Brunswick 4:339); and second, everywhere outside of the longest-built dikes the marsh is built up higher, even to two feet or more, than it is inside the dikes. Since the marsh was built as high as the tides could reach before it was diked, the land must have sunk to allow it to build so much higher now, even allowing for some sinking of the marsh through the removal of its mineral matters with the crops. Further, the ease with which the tide floods old marsh when admitted, building it up a foot or more, seems explicable only in this way. A case is known on the Tantramar marsh where a large ditch diked upon both sides was neglected, when it filled itself up with mud to a height of two feet above the surrounding marsh.

[10] The percentage of mud in the water is not so great, however, as it appears and as popularly supposed. To the eye it seems often to be little more than "liquid mud." By use of a graduated measuring glass on the end of a long cord I have taken samples from the bridges at various places, which, after settling, allowed the percentage of mud to be determined exactly. I have found the greatest amount in the rivers emptying out at low water, when it rose to an extreme of 4%, and it ranged at other times and places from that downward. At flood tide I have nowhere found it reaching 2%.

carried up their course instead of down. This wandering of the rivers explains many marsh phenomena otherwise very puzzling, such as the occasional miniature cliffs in the high marsh, and the layers of peat or blue mud (both formed only in presence of fresh water away from influence of the tide), exposed by canals, or even by the river itself, which thus reaches places formerly far removed from it.[11]

When the waters spread over the marsh, they of course drop most of their mud, and particularly its coarser parts, on and near the banks, thus building the marsh higher there than elsewhere. Hence the drainage of the fresh water, falling on the marshes as rain or draining upon them from the upland, is obstructed, and it tends to accumulate in the lowest places, viz., those farthest from the rivers, and hence near the upland or in basins between rivers. This fresh water allows the development of a fresh-water vegetation which initiates the formation of true bog, a point of immense importance in the ecology and economics of the marsh-vegetation. Again, at the head of tide in the rivers, the incoming salt water meets the outgoing fresh water and drops its sediment. Thus the rivers are tending always to dam themselves up at the contact of salt and fresh water, and they would doubtless do so completely were it not for the scouring out of the channel by the fresh water when the tide is out. The heads of the rivers, too, show another important phenomenon, viz., the level of high tide is higher there than at their mouths owing to the tendency of tidal rivers to pile up their waters on account of the inertia of their rush.[12] It hence comes about that the marsh is actually higher at the head of a river than at its mouth and the highest part of a marsh is at the

[11] It explains also the presence of concentric lines of old French dikes at Prospect Farm on the Aulac, and probably elsewhere, and the fact that the Misseguash is not now in the same position at Pont à Buot which it has on the very detailed maps of Franquet in 1754. It leads also to the occasional abandonment of pieces of marsh too small to be kept diked profitably.

[12] Mentioned in all works on tidal rivers. I have been told, as a good example of it, that the railroad levels show the high-tide level of the Petitcodiac to be higher at Salisbury than at Moncton; and Dixon and Trueman mention that at the big oxbows on the Tantramar, at very high and rising tides the water pours back over the neck into the river again.

head of the tidal parts of its rivers. This is finely shown by the levels taken on the Misseguash by the engineers of the Marsh Company, of which a condensed compilation is given herewith (*fig. 3*). Where the heads of the rivers wander, as they are particularly liable to do on account of the struggle between the fresh water and the dam at head of tide, a large part of the marsh may be thus elevated at tide-head, and in consequence the drainage above it is greatly obstructed. This results in a great accumulation of fresh water, with a consequent formation of immense bogs; and thus have originated the great bogs at the heads of the Tantramar, Aulac, Misseguash, and LaPlanche.

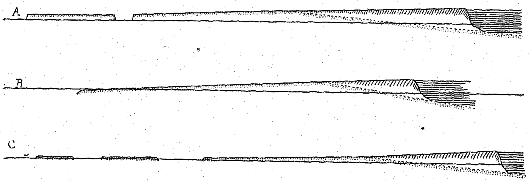


FIG. 3.—True levels on marshes and bogs determined by spirit-level; condensed from the plans of the Misseguash Marsh Co. Marsh is dotted and bog is shaded. The horizontal line is average high water in Cumberland Basin. Breaks in the marsh are where the levels ran along the river. Vertical scale 40 feet = 1 inch; horizontal ½ inch = one mile. *A*, from the Misseguash River near the railroad to Round Lake (*fig. 2*). *B*, from the La Planche River near the railroad to Long Lake; *C*, from Cumberland Basin to Long Lake.

Bogs therefore exist along the margin of upland, between rivers in the same basin,[13] and at the heads of rivers. Their extent, and their position relative to the cultivated and salt marsh may be learned from the accompanying map (*fig. 2*). In a general way the head of tide on the rivers, that is, the highest part of the marsh, marks the transition from marsh to bog; above this point, the rivers are fresh-water streams meandering through bog and expanding here and there into lakes.

The merging of the marsh into bogs is of course very gradual, and it is a well-known fact that the marsh mud extends every-

[13] Of which a perfect example occurs in the "Sunken Island" between the Tantramar and the Aulac (*fig. 2*).

where beneath the bog, even beneath the great bogs at the head of the tidal rivers. Soundings through the bog are easily made, and they show that the depth of the surface of the marsh mud from the top of the bog increases from nothing at the head of tide down to 6 or 7 feet away from the high part. Not enough soundings are available, however, to prove whether or not the slope is gradual from the high marsh to the extreme heads of the bogs, but so far as they go the soundings show this to be in general the case. This is confirmed by the water levels in the canal of the Misseguash Marsh Company. Where the canal

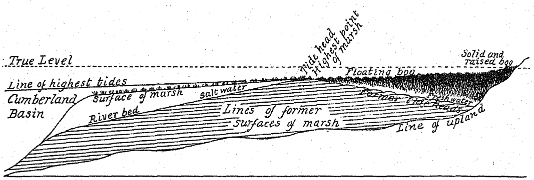


FIG. 4.—Ideal longitudinal section the marshes from sea to upland, to illustrate their origin.

passes through the highest part of the marsh near Black Island, the surface of the mud in July was nearly three feet above the water level; two miles up the bog, however, with a very slight current in the canal, the surface of the mud had dipped under the water, and the slope between the two points was perfectly gradual. It is fair to conclude therefore that the surface of the mud slopes away continuously from tide-head to the extreme distal margin of the bog. The question now arises, why this slope, which carries the bottom of the bog much below high-water level? No doubt the answer is to be found in the subsidence of the land already spoken of. Each part of the under-bog mud must at one time have been the tide-head and the highest part of the marsh; the newer tide-heads would be nearest the present one, and they would be progressively older, and hence have been carried deeper by the subsidence, the farther they are from the present one. This condition is diagrammatically represented in *fig. 4*.

The origin of the great bogs is thus made plain, but why are they mostly of the floating type? They are in fact almost entirely of this kind, though in places they are solid, and even approximate to the raised or *Hochmoor* type. They quake when one walks upon them, and a stick thrust through them penetrates from one to four feet of moss, then goes through a foot or two of water and soft organic mud before reaching the solid marsh mud. The foot or two of water seems to be fairly constant everywhere except in the shallowest parts, while the thickness of the mat of floating moss increases from the shallower towards the deeper parts, as illustrated diagrammatically in *fig. 4*. The levels (*fig. 3*) also show that the surface rises as the bog grows thicker, as is to be expected. It is a general rule in bog-formation over large basins that the floating bog is the first stage, and this is followed, as a result of growth and compacting, by solid bog, which in turn is succeeded by the raised or *Hochmoor* type. It may be a fact, therefore, that the floating character of these bogs is due to their youth—they have not yet had time to form the solid and raised types except on their oldest parts, around the margins and at the heads of the bog rivers, where such types do in fact occur. On this explanation one at first thought attributes the numerous lakes to places which the bog has not yet overgrown. But this explanation is in several respects not satisfactory. The facts seem to show that the growth of bog has been continuous from the upland outward to the marsh. Moreover, the lakes are always deeper than the surrounding bog. It seems, therefore, that there must be some positive factor tending to keep them open.[14]

[14] Possibly it may be connected with the presence in those places of a sufficient supply of salt to prevent the formation of the strongly salt-shy (halophobous) bog vegetation. As the efflorescence of salt on the mud thrown up from deep in the bog by the dredge of the Misseguash Company shows, some salt still exists in the mud beneath the bog water. This must be slowly dissolved out by the bog water, and the solution would settle towards the deepest places, which are the lakes, and might accumulate there to an extent sufficient, when stirred up by the waves, to keep them open of vegetation. The meaning of the deeper places over which the lakes lie is not so plain, but probably they represent in part portions of old river channels. This possible presence of some salt in the bottom water of the bog cannot, of course, explain the floating character of the bog, since the lower layers of vegetation are dead and unaffected by it.

A physiographic fact of some interest about the lakes may here be mentioned.

Economics of the marshes.

I. *Crops and prices.*—When reclaimed from the sea the marshes are wonderfully fertile, and in this respect they are unsurpassed, if they are equaled, by any land in eastern Canada. They are not, however, equally good for all crops, but are best for grasses and grains, to which consequently they are almost entirely given up; root crops will grow upon them, but not to advantage. They form also extremely rich pasturage, and to some extent are used for this purpose. The grasses which grow upon the best parts are the usual upland English hay grasses, which become very tall, very dense, and of very superior quality, luxuriant but not rank, producing easily three tons and upwards of the best hay to the acre. In less well drained places, coarser grasses grow, but these too are of good value. No attempt is made to take two crops a year, though some farmers allow their cattle to fatten on the rich aftermath. No fertilizers of any sort are placed upon the marshes, and the only cultivation consists in an occasional plowing, on an average once in ten to fifteen years, when a single crop of oats is sown, after which the land is brought at once into grass again.

The fertility of the marshes depends upon two, perhaps upon three, features. First there is the presence of the substances and conditions necessary for the perfect nourishment of the crop, as shown by its luxuriance. Second, the fertility is extremely lasting. The best marsh may be cropped with unlimited yield for decades together without any return to the soil. There are places on the Aulac, which are known absolutely not to have been renovated in any way since 1827, and are believed not to have been treated in any way for fifty and perhaps a hundred and fifty years before that, which are bearing today crops as bountiful as ever. There is on this river, at Prospect farm, a small triangle, known not to have been even plowed for over forty years, which has never ceased to bear a luxuriant crop of the best English hay grasses. These are of course among the

Some of them are in contact, particularly on their northeastern margins with the uplands and have there gravelly beaches. This is no doubt correlated with the prevalence of strong southwest winds in the region, which cause a surf on the northeast shores unfavorable to the development of bog vegetation.

best places; but there are parts, particularly on the marsh longest reclaimed, which show more or less exhaustion.[15] Such marsh may have its fertility largely restored by fresh mud brought in by the sea when allowed behind the dikes. Third, the water conditions of the marsh soil are such that the vegetation is somewhat less affected by dry seasons than is that of the uplands, and a bad hay year for the uplands is not so bad for the marshes. The causes of all these peculiarities in the marsh fertility will be discussed later.

The result of this combination of good qualities is, naturally, to give the marshes a high value. Marsh situated near the towns, and well-placed for drainage, is worth upwards of $180.00 to $200.00 per acre; there are large areas valued at $100.00 an acre, while prices range, of course, from these downwards.

II. *Mode of reclaiming the marshes.*—The original marsh as built by the sea bears a sparse vegetation of typical salt marsh plants, of which only a few of the grasses, and these to a limited extent, are useful. To reclaim this marsh three things are needed: (1) to shut out the sea, (2) to wash out most of the salt, (3) to provide for the removal of the fresh water falling as rain or draining from the upland. The sea is shut out by dikes of the usual sort. These are triangular in section, built of the marsh mud itself, often with a core of stakes and brush. Against the open sea they may be six feet high, and they are protected from the wash of the waves by lines of stakes or piling and loose stones; but along the rivers they are much lower, for up the rivers the marsh itself is progressively higher. The removal of the salt takes place naturally by action of the falling rain, which washes it through the drains into the sea. It requires three to four years in newly reclaimed marsh to do this sufficiently to allow the more useful grasses to grow, and during this time there is an entirely natural succession of plants accompanying the freshening, whose kinds and sequences will presently be discussed. To allow the rain-water to drain off is all-important, not only for removal of the salt and for proper aeration of

[15] This is not to be confused with degeneration through bog-formation on account of defective drainage, a common but morphologically very different phenomenon.

the soil, but also to prevent the ever-present tendency to formation of bog plants. This drainage is accomplished by a system of open ditches, which, small and only a foot or two deep away from the rivers, are much larger and deeper near them, partly to give a fall and partly because of the greater height of the marsh there. At the outlets of these ditches on the rivers the fresh water is allowed to drain out by an arrangement that does not allow the tide to enter, namely, by placing under the dike a wooden "sluice" in which hangs a "clapper," hinged at the top and inclining outwards toward the river at the bottom (*fig. 5*). When the tide is out, the pressure of the fresh water

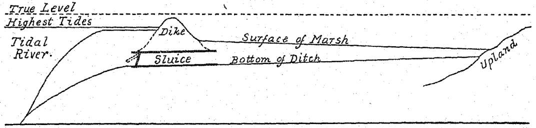


FIG. 5.—Diagrammatic cross-section through the marsh from tidal river to upland, showing a sluice.

opens this; when the tide rises its weight tightly closes it. Of course the fresh water then accumulates in the ditches, but never for long, for the sluice is not far below high-water mark. These sluices and clappers last indefinitely, apparently preserved by some antiseptic action of the salt water. A sluice of this kind is used not only in the ditches but frequently in a dike thrown across an entire river, as in the case of the Aulac. The entire structure, dike and sluice, is then called an "aboideau," and such a river is said to be "aboideaued."[16]

[16] A word introduced by the Acadians from Saintonge, France, where it is still used in the form *aboteau*. Its origin is fully discussed in the New Brunswick Magazine 1 : 225, 226, 284, 340, and 3 : 218. Naturally some other peculiar uses of words have grown up in the marsh country. Thus, the word tide is used for the salt water itself, and one often hears "let the tide on the marsh." Also the word is used constantly as a verb, as "They intend to tide the marsh," *i. e.*, to let the salt water on it, and "It was tided last year." The word ditch is used also as a verb. A large section of marsh surrounded by a single dike is called "a body." In Nova Scotia, the word dike is applied to the marsh itself (no doubt abbreviated from "diked land"), while the dike is called the "running dike," but the usage in New Brunswick is as in this paper. The word *marsh* itself is rather a misnomer and is said locally to do the country some damage by giving an unfavorable impression of its character.

The process of flooding a piece of land that has degenerated through cropping, or through bog growth as a consequence of neglect of drainage, is simple. The dikes are broken down at convenient places, and the tide is allowed to flow at will over the old marsh. Bog vegetation is killed immediately by the salt water, and it, as well as the entire marsh surface, is soon covered with several inches to a foot, or even more, of new mud. This requires from one to three years according to the situation of the marsh.[17] The dikes are then rebuilt, ditches are opened, the vegetation goes through its usual cycle, and in from two to four years it is again bearing rich English hay. This flooding, however, is by no means as extensively used as it should be, for many owners are unwilling, or cannot afford, to lose all return from their land for several years. Sometimes an attempt is made to flood and obtain crops simultaneously, by admitting only a little tide at a time, or by admitting it only in late autumn after the ground is frozen, when the grasses are little injured by it. But such compromises are considered not to pay in the end.

The struggle with the fresh water is incessant, and is the greatest care and expense of the marsh farmer. Poor drainage soon leads to the replacement of the valuable English hay by the less valuable sorts, which in turn yield to yet coarser kinds, the series ending in the appearance of useless sphagnum mosses and bog plants. Abundant and intelligent ditching is the only remedy. Farmers differ so much, however, in willingness or ability to face this problem, that areas alongside of one another under similar natural conditions with but a ditch between differ greatly, one bearing the richest English hay, and the other only the coarser kinds.[18]

[17] It seems remarkable that no attempt has been made to hasten this process by utilization of the powerful currents of the rivers to turn wheels which could pump the water and mud upon the land. Such wheels are used in other countries for irrigation purposes.

[18] There is, however, another difficulty, much more serious, which greatly hampers both the struggle with the bog and the renovation of old and exhausted marsh. The dikes are built and maintained at the common expense of a large number of owners of marsh land, and enclose a huge "body" of marsh. Owing to differences of location and of treatment, some parts of such a body come to need tiding while others do not, and

So much for the reclamation and renovation of the marshes. In addition there has grown up within a century a most important practice of reclaiming and converting into marsh both the lakes in the bogs and the bogs themselves. Its principle is simple, though the practice is by no means so. Canals are dug from the tidal rivers into the lakes, whereby the latter are drained and the tide is allowed to enter with the rich mud. In this way a lake may be entirely filled with mud and become the richest of marsh, and this has been done in the several lakes shown by the red lines on the detailed map (*fig. 2*). After the lakes have been thus reclaimed, the surrounding bog is attacked. The salt water turned upon the bog kills at once all vegetation, which compacts, sinks, becomes covered with marsh mud and gradually comes into rich marsh. Immense areas have thus been reclaimed on the Tantramar system, as shown upon the map above cited, and the process is steadily going on, while a systematic attempt is being made by the Misseguash Marsh Company to reclaim on a large scale the lakes and bogs on the Misseguash. In such operations the most constant care is needful to prevent the canals from damming and filling themselves up, and this is mainly accomplished by utilizing the outward rush of the fresh water to scour out the channels. The great aim, therefore, is to secure the greatest possible "rush of tide up, and of freshet down." There are marsh farmers who have become very expert in lake and bog reclamation, to their own profit and the good of the community. I believe this process of reclaiming bog, here practiced, is entirely unique.[19]

An important feature of the economics of the marshes is the aboideaued rivers, already explained, of which the Aulac is by

there are all gradations between. Disputes then arise among the owners of the body as to the course to be pursued, which often go so far that nothing at all is done, and great stretches of marsh suffer so severely as to become of little value. This is most markedly the case on parts of the Shepody marshes, large areas of which, capable of the highest development, are lying nearly ruined through the inability of the owners to co-operate for the common good. It would seem proper for the local legislature to interfere in such cases, where not only the interests of some owners are concerned, but also the prosperity of the neighboring region.

[19] The process is more fully described in the papers by Crawley, by Goodwin, and by Trueman, cited in the bibliography.

far the best example. An aboideau, shutting out the tide while allowing drainage of fresh water, recovers at one operation, without the expense of river-dikes, all the marsh along the river above it, and also the banks of the river and much of its bed, both of which, but especially the banks, produce the very richest of hay. At first sight it might seem wise to aboideau all rivers at their mouths, but when it is remembered that no land above the aboideau can be renewed by the tide, nor can any bog or lake be reclaimed, it will be seen that an aboideau is only profitable on streams which have no bog nor lake at their heads, and which have a soil so deep as not to need renewal. This is true of many smaller streams heading against upland, but of none of the rivers excepting the main Aulac. An aboideau upon the Tantramar would have prevented the reclamation of thousands of acres which are now productive. Naturally, therefore, there is much jealousy of aboideaus upon the part of those who own inferior marsh or bog above them, and the words of a local writer,[20] who calls them "the curse of our rivers," reflect a common opinion.[21]

[20] MR. WM. FAWCETT, of Upper Sackville, in newspaper articles.

[21] The marshes were first reclaimed by the Acadian French, who began the work in 1670 and continued it, raising much grain, until expelled by the English in 1755. They developed the methods of reclamation (of marsh, but not of bog) still in use, and many of their old dikes are still to be seen. The extent of their operations is well shown upon several maps of the time (particularly on "A large and particular Plan of Chignecto Bay," 1755), and its limits are marked by the fine dotted line drawn on the accompanying detailed map (*fig. 2*). The lands lay vacant from 1755 to 1760, after which they were regranted to New Englanders and English, and their settlement and reclamation has continued steadily to this day. In 1827 the Aulac was first successfully aboideaued, as were later the Misseguash and the La Planche, though from both of the latter the aboideaus have since been removed. No attempt was made to reclaim bog and lake until early in the last century, when a farmer of Upper Sackville, Toler Thompson, whose name is justly held in high honor in the vicinity, after long study of the tidal currents and bog levels became convinced that the lakes could be filled and reclaimed. It was long before others could be convinced, but finally a canal was dug from the Tantramar into Rush Lake (*fig. 2*) which quickly became rich marsh. Later Goose Lake was recovered, and later Log Lake (which required fifteen years to fill with mud), while Long Lake, Ogdens and others are now being filled, and thus the system initiated by Thompson is adding immensely to the wealth of this region. On the Misseguash little had been done, but five years ago a company "The Misseguash Marsh Company" was organized to attempt to do with ample capital, systematic methods, and favorable legislation, what had been done piecemeal

One other phase of the economics of the marshes remains to be mentioned. They are absolutely healthful. No malaria nor other disease is known about them. There is a local tradition that men have died from drinking the bog water; but I am told by a local physician that cases of typhoid fever are referred to and that these were probably contracted in quite another way.

The importance of the ecological study of the marsh vegetation.

From a systematic or floristic point of view these marshes are of slight botanical interest. They contain no species that are peculiar to them, out of range, or otherwise remarkable. The plants of the unreclaimed marshes, and also of the bogs, are those ordinarily occupying such situations in this part of America, while the fully reclaimed marsh is but a good hay meadow, bearing grasses altogether like those abounding on the cultivated uplands round about. Yet from another, namely, the ecological point of view, the marsh vegetation is replete with scientific interest, for the marked gradations of physical conditions of soil and water within a limited space, and, owing to artificial changes, within a limited time, allow us a rare chance to trace upon a large scale the effects of those important conditions upon the plants, and to draw some conclusions as to the nature of the adaptation of the one to the other. It is necessary, first of all, to study carefully these, and other, physical factors to which the plants must respond; then we may trace the responses in the plants.

The factors determining the ecological features of the marsh vegetation.

The principal ecological factors, as arranged in Schimper's comprehensive work, *Pflanzengeographie auf physiologischer Grundlage*, are the following: *Water*, *temperature*, *light*, *air*, *soil*, *animals*

on the Tantramar. This company is now vigorously at work, and it is hoped that their efforts to convert the thousands of acres of useless bog on this river into productive marsh will be entirely successful.

The best account of Toler Thompson and his work that I have seen is in an article by Judge Botsford in the *Chignecto Post* in January, 1886. Another valuable article on the history of marsh reclamation is that of Mr. Howard Trueman in the *St. John Sun* in late December, 1897.

(including the aggressive *man*). To these should be added another of great importance, *geography of the basin.*

Water.—Of all the factors determining plant form and distribution, this is the most important. We consider first the precipitation of the marsh country. No records are available for the immediate vicinity, but it may be inferred from the amount in places surrounding the region. Thus, according to the rainfall map published in 1899 to illustrate the presidential address (by T. C. Keefer) before the Royal Society of Canada, the mean annual rainfall is: at Moncton, N. B., 44.96^{in}; at Truro, N. S., 43.28; at Charlottetown, P. E. I, 41.45, while at St. John, N. B., it is 47.38^{in}. The marsh country, lying at the head of the Bay of Fundy, and directly in line with it, probably has less rainfall than St. John, but more than any of the other localities; and hence we may fix it conservatively at 45^{in}.

As to its distribution through the year, the only available records are for St. John, where it is as shown in the following table, "for a long series of years," supplied to me by the Dominion Meteorological office at Ottawa:

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
5.55	3.93	3.80	2.50	3.66	2.72	3.29	4.64	3.08	4.13	4.71	5.16	47.17^{in}

Diminished *pro rata* for the lesser total rainfall, this table represents proportionally, no doubt, the distribution of precipitation through the year at the marshes.

It thus appears that the marshes have a precipitation ample for the development of an abundant temperate-region vegetation, and that it is distributed fairly evenly through the growing season of the year.

As to prevailing humidity of the atmosphere, there are no records available even at St. John. But since there is much cloudy weather, no little fog and mist, almost insular conditions, and very constant southwest winds blowing over the entire length of the Bay of Fundy, the humidity must be rather high.

Turning to the influence of water in another way, its mechanical effects, several points are to be noted. One is the very impor-

tant result arising from the abundant precipitation in connection with the poor drainage, leading to the formation of the immense bogs later to be considered. The presence of ground water in soil is usually important, but it here plays little or no part, as will be pointed out later. Another effect is in the scattering of seeds by means of currents. It would seem that the tidal currents in the rivers must form efficient disseminators of the seeds of at least the salt-plants. I have made a test of this by bringing back from the marshes several samples of the newly-deposited marsh mud, which the next spring were given very favorable conditions for the germination of any seeds in them, but no plants appeared. It may be that none were present in summer, and autumn samples might give a different result. There is, however, another mechanical effect of the tidal currents of considerable importance, namely, although they have built up the marshes entirely, they keep the river banks so constantly shifting, laying down mud in some places and scouring it out in others, that no vegetation is able to gain a foothold below the quieter zone near high-tide marks, excepting in the case of the curious sedge bogs, which I do not entirely understand; and these great banks are bare of all plant life excepting an occasional diatom swept from the sea. These banks and flats must be the largest areas barren of life in all northeastern America.

Temperature.—Next in importance to moisture as an ecological factor, is temperature. I have been unable to secure a copy

	January	February	March	April	May	June	July
Mean highest	28.2	27.6	34.3	46.4	57.2	64.4	68.8
Mean lowest	9.0	9.7	18.3	30.8	40.4	48.3	53.2
Mean temperature	18.6	18.7	26.3	38.6	48.8	56.3	61.0
Mean daily range	19.2	17.9	16.0	15.6	16.8	16.1	15.6
Absolute highest	50.0	49.0	52.0	71.7	75.0	86.7	88.9
Absolute lowest	−21.0	−15.0	−10.0	12.0	27.0	35.0	41.0

	August	September	October	November	December	Year
Mean highest	68.8	63.3	51.8	43.3	32.4	48.9
Mean lowest	53.7	47.8	37.6	28.9	15.1	32.7
Mean temperature	61.3	55.6	44.7	36.1	23.7	40.8
Mean daily range	15.1	15.5	14.2	14.4	17.3	16.2
Absolute highest	85.0	85.0	72.4	61.0	54.5	88.9
Absolute lowest	43.0	32.5	21.4	− 1.5	−19.5	−21.0

of the records kept in Sackville in the marsh country, and must turn therefore to those of St. John. The above table, based on the averages for a long series of years, is supplied by the Dominion Meteorological Office at Ottawa. Owing to well-known local conditions, the summer temperatures average lower, and the winter higher at St. John than elsewhere in the province, and this correction must be applied to the table to make it of use in estimating the conditions of the marsh country.

It is important to note further, that on the marshes themselves the snowfall is said not to be great, and often for considerable periods in winter the ground is bare. This condition, combined with the strong winds that prevail there and the total lack of shelter on the marshes, makes the winter conditions unusually unfavorable for vegetation, which must consist of plants able to endure such trying conditions. For this no arrangement is better than that of the grasses, which largely retreat to or under the ground in winter. On the other hand, at times in summer, the marshes, lying at sea level and completely unshaded, receive so strong an insolation as to become very hot, though this is never long continued.

Light.—The latitude of these marshes is 45° 50′ to 46°, from which the amount of light they would receive if unshaded by clouds, etc., and with a clear atmosphere may be estimated. But the full amount is much diminished by cloudy weather. No records of cloudiness are kept nearer than St. John, where the percentages for a long series of years are as follows:

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
53	54	60	55	61	62	63	62	53	58	60	59	58

Probably the cloud percentage for the marshes is not very different from this, though it would be less rather than more, say 50 per cent. for the year, 55–60 per cent. for the summer months. No records whatever for intensity of the light are available. It is important to note, however, that the marshes, perfectly level and unshaded, receive the full value of what light there is.

Air.—Here as elsewhere, chemically the air is hardly an ecological factor; at all events it is not a differential factor. Atmospheric pressure on the marshes, lying at sea level, is of course at its maximum, but the daily fluctuations of the barometer, as Schimper remarks, have no known effects upon the form or distribution of vegetation. Mechanically, however, as it moves in winds, the atmosphere is here important. Unfortunately no official meteorological records are available for direction or velocity, but a record of another kind is visible and unmistakable, namely, the wind effects upon the vegetation. As I have elsewhere pointed out,[22] the trees and shrubs on the neighboring ridges and in places on the margins of the bogs are strongly bent to the northeast, and show a great development of branches on that side, with an abortion on the southwest. This is caused by the very strong southwest winds which prevail here, as the residents agree, during most of the year, a phenomenon resulting from the position of the marshes in relation to the Bay of Fundy. This great bay lies northeast and southwest, and is of the form of a huge funnel. Wide at its mouth, it narrows between walls of increasing height (300 to 700 feet or more) towards its head. At Cape Chignecto the northern branch, with which we are concerned, continues and even intensifies this funnel character, ending finally in the low-lying marsh country. The great winds here are due to very much the same causes as the great tides. Every wind from a southerly direction is thus brought into a southwesterly course, condensed, strengthened, and poured over the low-lying marsh country, and the vegetation must be of a kind to endure it, for which nothing is better than the grasses.

It might be expected, as a result of the prevalence of these winds, that dunes would be formed on the unreclaimed marshes. There is, however, not the least trace of this, chiefly because the mud when laid down by the tide hardens as it dries, allowing the wind no hold upon it.

The constancy and strength of the winds on the marshes must greatly promote evaporation (transpiration) from any

[22] Bull. Nat. Hist. Soc. New Bruns. 4: 134.

vegetation there, not only in the summer, when an abundance of water is usually available for the vegetation, but in those critical periods of winter and early spring, when, owing to the low temperature of the soil, water is not readily absorbed.

Another important influence of wind upon vegetation consists in its effects upon cross-pollination and dissemination. Obviously the conditions are particularly favorable for wind-pollination on the marshes (and by that very fact somewhat unfavorable for insect-pollination), and the same is true for wind dissemination. We shall see later how much the vegetation is influenced by these factors.

[*To be continued.*]

GEOGRAPHIC DISTRIBUTION OF ISOETES SACCHARATA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LI.

GEORGE HARRISON SHULL.

(WITH MAP)

WHILE making a study of the aquatic vegetation of Chesapeake Bay for the U. S. Bureau of Plant Industry during the summer of 1902, I located several new stations for *Isoetes saccharata* Engelm. This species has had an interesting history, and as our knowledge of its range has greatly increased within the last few years, I have thought it desirable to publish the accompanying map showing the exact distribution as now known, to give a detailed account of its history, and to discuss briefly several problems which have presented themselves for solution.

For a quarter of a century *Isoetes saccharata* Engelm. was known only from its type locality on the Wicomico River and from the Nanticoke, which empty into the bay by a common mouth opposite and a little north of the mouth of the Potomac. Far up the Wicomico, about a mile below the town of Salisbury, Maryland, the plant was first discovered by William M. Canby in 1863. The material was submitted to Dr. Engelmann, who was at that time the highest American authority on the genus, and was first described by him in Gray's *Manual*, 5th edition, p. 676, 1867. In 1874 Canby found a second station at Seaford, Del. Not until 1888 was it collected at a third station, when it was found by Vasey and Coville near Alexandria, Va., in Hunting Creek, a tributary to the Potomac. The material obtained here was not recognized for some years as identical with Canby's material, and was referred by Theo. Holm to *Isoetes riparia* Engelm.[1] The next year Coville found it at Mount Vernon on the Potomac, but this collection seems to have been overlooked

[1] Proc. Biol. Soc. Washington 7:132. 8 Ap 1892.

by Holm, and was not published until in 1900, when it was mentioned in the *Sixth List of Additions to the Flora of Washington*.[2]

Not until 1893 were specimens recognized as *Isoetes saccharata* Engelm. secured away from Canby's stations on the Wicomico and Nanticoke Rivers. In this year T. Chalkley Palmer discovered it near the western end of the Delaware and Chesapeake Canal in Back Creek, a tributary to Elk River, nearly 140^{km} north of the type locality. During the next two years he discovered it at several other points in both Elk and Sassafras Rivers. These collections formed the subject of an interesting account published in the BOTANICAL GAZETTE in 1896.[3]

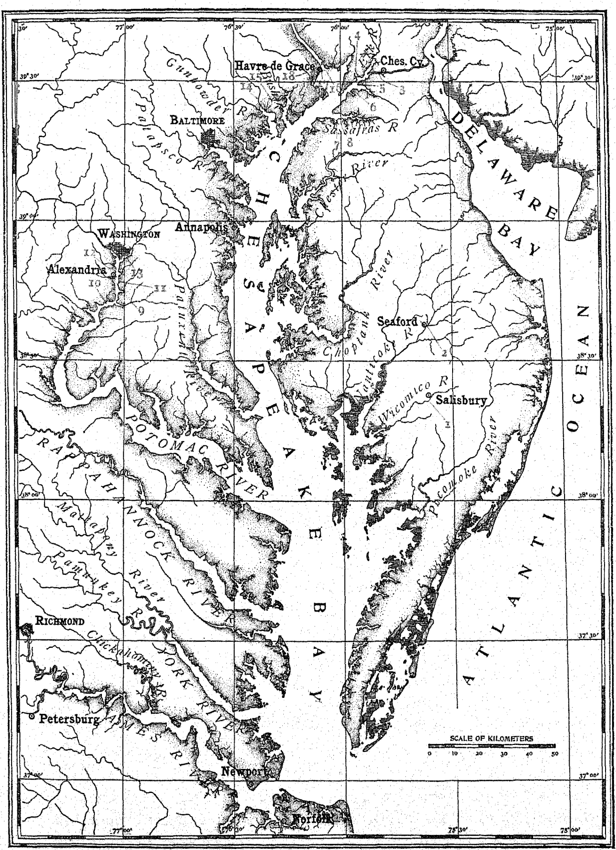
The only new stations which have been published since Palmer's account are given in the *Sixth List of Additions to the Flora of Washington*,[4] where, besides the reference to Coville's Mount Vernon station above mentioned, two new localities are recorded for the upper Potomac. Along with the publication of these stations were given the descriptions of two new varieties: var. *Palmeri* A. A. Eaton, based upon Palmer's material from Lloyds Creek, Sassafras River; and var. *reticulata* A. A. Eaton, based upon several collections, including that of Vasey and Coville (1888) from the Hunting Creek station, Alexandria, Va.

Since the publication of Palmer's paper on Isoetes, that collector has located several new stations which are here published for the first time. The most notable of these, and the only one outside of the Elk and Sassafras Rivers, is about 25^{m} north of the Havre de Grace light at the mouth of the Susquehanna River, and therefore at the very head of the bay.

I believe these are all the localities known for the species before my collections of the past summer. My work was limited almost entirely to the west side of the bay, and my collections of *Isoetes saccharata* were made in the western tributaries and along the shore of the northern part of the bay, my most northern station being only 500^{m} from Palmer's Havre de Grace station, thus making the circuit about the head of the bay virtually complete.

[2] Proc. Biol. Soc. Washington **14**:49. 19 Je 1901.

[3] BOT. GAZ. **21**: 218–223. 1896. [4] *Loc. cit.*



EXPLANATION OF MAP OF CHESAPEAKE BAY.—Adapted from Coast Chart number 376 of U. S. Coast and Geodetic Survey, and McGee's Drainage Map of the Middle Atlantic Slope (U. S. Geol. Survey, Seventh Annual Report, *pl. 57.*) Stations for *Isoetes saccharata* Engelm. are located at the points in which the index lines cut the shore lines.

So far as could be determined, the index lines are perpendicular to the portion of the shore occupied by the Isoetes.

It will be seen then that within the last ten years *Isoetes saccharata* and its forms have been traced from its original station completely to the head of the bay. Wicomico River is yet the most southern station known, but it is not improbable that a careful exploration will result in its discovery in the fresh-water estuarine portions of the more southern tributaries of the bay.

For the sake of completeness and to facilitate further study of the several colonies now known, as well as to serve as an index to the map, I insert the following list comprising all the known stations, with such data as I have been able to gather regarding each. The figure preceding each name agrees with the corresponding station as indicated on the map. In each case the station is at the point in which the index line intersects the shore line.

1. *Salisbury, Md.*—On a label in the herbarium of G. Engelmann, St. Louis, Mo., now in the Missouri Botanical Garden, the type locality is described thus:[5] "Shores of Wicomico River, one mile [1.6^{km}] below the town of Salisbury, eastern shore of Maryland, on gravel, covered by a thin layer of mud deposited by the tide; alternately covered and exposed by the tide. . . . . Growing in the society of *Sagittaria pusilla* (*S. subulata* [L.] Buchenau), *Tillaea simplex* (*T. aquatica* L.), *Hemianthus micranthemoides* (*Micranthemum micranthemoides* [Nutt.] Wettst.) etc.; first found Sept. 15, 1863. Wm. M. Canby." This label, which bears the date September 8, 1866, evidently belongs to a type specimen. In a letter to the writer, Canby explains that the original station is a sandy or gravelly slope on the south side of the river.

In September 1895 T. C. Palmer, in an attempt to visit the type locality, found the species growing at Williams Point on the Wicomico River.

2. *Seaford, Del.*, is situated at the confluence of the north and south branches of the Nanticoke River, and only 5^{km} below the head of tide water. A label in the Engelmann herbarium,

[5] A similar but somewhat ambiguous description of the type locality occurs in Engelmann's paper on "The Genus Isoetes in North America." Trans. St. Louis Acad. Sci. 4: 382. 1882.

belonging to one of the original specimens from this station reads: "Muddy and gravelly shores of Nanticoke River near Seaford, Delaware. Wm. M. Canby, Wilmington, Del., August 1874." That this was the first collection at this station is shown by the fact that duplicates in the U. S. National Herbarium and in the Herbarium of the Field Columbian Museum bear the statement that it is "a new station." The area occupied by Isoetes at this place is located "nearly opposite the town, a little above it, in fact. The space there is not very large, perhaps 100^{ft}"[6] (30^{m}).

3. *Back Creek*, tributary to Elk River, eastern shore of Maryland. This station is on the south shore of the creek about 3^{km} from the western end of Chesapeake and Delaware Canal and nearly 1^{km} below Chesapeake City. The first collection was made by T. C. Palmer in August 1893. He made further collections the following year and published a short statement in the BOTANICAL GAZETTE.[7]

4. *Piney Creek Cove* is a broad indentation in the north shore of Elk River $9\text{–}11^{km}$ from its mouth. On August 13, 1894, T. C. Palmer collected *Isoetes saccharata*, just below the mouth of the small stream which empties at the northeast angle of the cove. This station was also mentioned with the last in the BOTANICAL GAZETTE.

5. *Town Point* is the upper angle formed by the confluence of Bohemia River with Elk River, into which it flows from the east. About 500^{m} north of this point Isoetes was collected on July 31, 1896, by T. C. Palmer. A specimen from this collection in the National Herbarium gives the habitat: "Tidal tract; gravel nearly bare." This station has not been previously recorded.

6. *Cabin Johns Creek* empties into Elk River from the southeast about 5^{km} above the mouth of the latter. A specimen in the National Herbarium bears the data: "July 21, 1896. Cabin John's Creek, Elk River. Tidal tract; gravel covered with mud. Collector T. Chalkley Palmer." This collection has not been published heretofore.

7. *Lloyds Creek* is a large shallow cove on the south shore of

[6] William M. Canby, in a letter. [7] BOT. GAZ. **20**: 32. 1895.

the Sassafras River, about 6^{km} east of Howells Point, and is nearly cut off from the river by a sand spit. On the south shore of this shallow bay, almost due south of its mouth, a very interesting collection of Isoetes was made by T. C. Palmer, August 12, 1895. The habitat as described on a label in the National Herbarium is characterized by "reddish sand capped lightly with mud." The material departed in a marked degree from typical *I. saccharata* Engelm., as was pointed out in the collector's interesting contribution in the BOTANICAL GAZETTE in 1896 (*l. c.*). In 1900, A. A. Eaton made this material the basis of his new variety *I. saccharata Palmeri.* In a letter to the writer, Palmer states that at none of his other stations does the Isoetes grow in such abundance as at Lloyds Creek.

8. *Turners Creek* empties into Sassafras River from the south about 4^{km} east of Lloyds Creek. On the south shore of Sassafras River just below the mouth of Turners Creek, a station, published here for the first time, was located by T. C. Palmer, July 18, 1897.

9. *Hunting Creek* empties into the Potomac River from the west immediately south of the city of Alexandria, Va. The highway from Alexandria to Mount Vernon is graded for some distance into the shallow part of the creek from each side, and crosses the middle part by a long bridge. The original station is a gravelly bed near the bridge on the right side of the embankment as the bridge is approached from the Alexandria end. The first collection at this place was made by George Vasey and F. V. Coville, July 22, 1888. It has been visited several times since, a recorded visit[8] having been made by W. R. Maxon, September 22, 1900. Maxon also collected at this station, September 7, 1901, a specimen of this date being placed in the National Herbarium. The writer secured specimens from the same place August 11, 1902, and also found it on the same side of the embankment which leads from the opposite end of the bridge toward Mount Vernon. These areas are not large, but the material is fairly abundant. The soil consists of pebbles covered with a layer of mud and the principal companion plant

[8] Sixth List of Additions to the Flora of Washington. *Loc. cit.*

is *Eriocaulon septangulare* With. The material collected at the Alexandria end of the bridge by Vasey and Coville, and Maxon's 1900 collection along with Steele's Anacostia material, soon to be mentioned, were made the basis of the new var. *reticulata* A. A. Eaton.

10. *Mount Vernon, Va.*, is on the west bank of the Potomac about 11^{km} south of Alexandria, Va. A specimen in the National Herbarium, collected at this place, bears the data: "Mt. Vernon, Va., July 4, 1889. Shore of the Potomac at the foot of the Mt. Vernon estate, Collector F. V. Coville." The collector describes (*in litt.*) the station as being "at the slope immediately in front of the house and therefore a hundred yards or more (100^{m}) north of the boat landing. There was a considerable area here in shallow water covered with Isoetes. The soil was gravelly."

11. *Notley Hall, Md.*, is on the east shore of the Potomac River, nearly opposite the mouth of Hunting Creek, Alexandria, Va. A specimen in the National Herbarium was collected at this place by F. V. Coville in 1894.

12. *Four Mile Run, Va.*—This creek enters the Potomac from the west about midway between Washington, D. C., and Alexandria, Va. Its lower course forms a wide bay, along the south side of which the banks are being eroded by wave action, which carries away the finer material, leaving a gently sloping tide-beach of mingled sand and gravel, on which Isoetes grows luxuriantly. The first collection at this station was made by E. S. Steele, August 5, 1898. The writer visited this place and made collections on August 22, 1902.

13. *Anacostia River* crosses the District of Columbia east of Washington, D. C., and empties into the Potomac River just south of that city. On September 1, 1900, E. S. Steele discovered Isoetes "on the southeast bank of the Anacostia River nearly opposite the Navy Yard, perhaps a half [one-fourth] mile below the Navy Yard bridge."[9] This collection forms a part of the type material of var. *reticulata* A. A. Eaton.

14. *Sugar Loaf Creek* is a small stream which empties into Gunpowder River, western shore of Maryland, from the north,

[9] In a letter to the writer.

at a point about 600^{m} northeast of Gunpowder station on the P. B. & W. R. R. On the small rounded point between Sugar Loaf Creek and Gunpowder River, I found *Isoetes saccharata* on September 2, 1902. The specimens were abundant but of small size, owing to the fact that they grew in a moderately dense colony of *Scirpus americanus* Pers., among which I have rarely found Isoetes elsewhere. Other associates of Isoetes at this station were *Lilaeopsis lineata* (Mx.) Greene, and *Eriocaulon septangulare* With. The soil conditions were typical—gravel covered with a thin layer of mud.

15. About 500^{m} above the mouth of Sugar Loaf Creek, on the east shore of Gunpowder River, I located another colony of Isoetes the following day, September 3, 1902. The specimens at this place were growing in a bed of sand only a few square meters in extent and were very thrifty.

16. *Havre de Grace Light* is on a small point on the west shore of the Susquehanna River at its mouth. The most interesting of T. C. Palmer's unpublished stations for Isoetes is a small area just north of this light house, near the pier. His collection at this point was made August 17, 1898, and is at present the northern known limit of the species.

17. *Havre de Grace Park* is along the shore of the bay, southwest of the Havre de Grace light. It descends to the bay by a steep bank, and below this bank, among the pebbles which pave the beach, I found the species growing abundantly, July 19, 1902.

18. Nearly 1^{km} west of the last, on the curved shore, known as the "knee" of the bay, *Isoetes saccharata* also grows, though not in such abundance as at the park station. I collected at this place also July 19, 1902, this being my first collection.

x. By this sign I have marked two points on Bush River at which single small specimens were found. The fact that these two specimens were seen indicates that its absence in notable quantity is due to unfavorable habitat, and not to barriers to its entrance. Although Bush River was explored from its mouth almost to the head of tide water, I did not see a single spot where I really expected to find it. The specimens found were evidently

choked by the density of the *Scirpus americanus* Pers., among which they grew. Where the shores were free from Scirpus, as they were for stretches north of Bush River station, P. B. & W. R. R., and at the mouth of Otter Creek, they were composed of pure gravel, subject to shifting with the action of the waves.

y. I have indicated thus the location of a well-grown specimen found floating in the bay at the mouth of Furnace Creek over 3^{km} from the nearest known colony.

It appears from this list of known stations that *Isoetes saccharata* has a general distribution in the fresh water portions of Chesapeake Bay and its tributaries, but is at present unknown from any other locality. If it has a wider distribution, our ignorance of that fact is not entirely due to lack of observation, for Delaware Bay, which furnishes the most accessible suitable habitats, has been explored by students of the genus, with the result that several stations have been located for *Isoetes riparia* Engelm., but not a single specimen of *I. saccharata* Engelm. has been found.

If the last named species is indeed limited to Chesapeake Bay, it will be of interest to consider the causes to which the restriction may be due. Endemic species have a peculiar interest in their bearing upon problems of biogeography. A cosmopolitan distribution is evidence of a high degree of adaptability to variation of habitat, and is also evidence either of an old species or of efficient means of dispersal. On the other hand, a species which is limited to a single locality is either a remnant of a once more widely distributed form, or it is a relatively new species which has arisen in the more or less isolated region to which it is now limited. In the first instance it has been protected by the barriers which surround it, or by peculiarly favorable conditions for its growth from the extinction which has overtaken the species in other regions; in the second case it has been prevented by barriers from spreading beyond the region of its origin. Cosmopolitan species seem to deny the existence of barriers, while local species not only confirm their existence but give a clue to the nature and position of these barriers. As biogeography has to do preeminently with barriers, it is evident

that species of local range are of the greatest importance in solving the fundamental problems of geographic distribution.

From this brief discussion it will be seen that there are two essentially different kinds of endemism. In one the species is a remnant, in the other it is a beginning. To the former of these the term *relict* endemism has been applied;[10] to the latter I shall apply the term *initial* endemism.[11] Relict endemism is illustrated by such classic examples as the Sequoia of western North America and *Ginkgo biloba* L. of eastern Asia. Initial endemism is perhaps best exemplified by numerous endemic species of oceanic islands, though it does not follow that all endemic species of oceanic islands are initial.

It is obvious that many difficulties will be encountered in determining whether any local species in question is a relict or an autochthon. It is also obvious that we may have initial species of a relict genus, though not the reverse. After examining the nature of the barriers which limit the distribution of *Isoetes saccharata* I shall suggest to which class of endemic species it probably belongs.

It will have been noted in examining the map, or in looking over the descriptions of the several stations, that even within the narrow confines of Chesapeake Bay, this species is not generally distributed along the shores, but occurs only here and there in closely limited areas, the largest of which is perhaps less than 100^m long. This extreme localization within its range is due solely to the requirements of its habitat. The chief conditions necessary for its success are the following:

a) It is limited to tidal beaches, which fact restricts it to a narrow zone, never more than a few meters wide along the shore

b) It requires fresh water, never occurring in water of more than slight salinity. South of Spesutie Island the rivers have a

[10] DRUDE, O., Handbuch der Pflanzengeographie 125. Stuttgart: J. Engelhorn. 1890.

[11] An initial species is called an autochthon and *autochthon* endemism might be used in contradistinction to *relict* endemism. Drude (*op. cit.* p. 124) refers to such species as "vicarious or corresponding forms," from which initial endemism is sometimes called *vicarious* endemism, but the significance of vicarious in this connection is too obscure to commend its adoption.

section near their mouths too salt for the growth of Isoetes, and this salt water section of the rivers becomes longer as we proceed toward the mouth of the bay. This isolates the suitable habitats in one river from those in neighboring rivers.

c) There must be sufficient stability of the soil of the shore to resist the action of the waves, and at the same time sufficient fineness of the soil particles to supply the needs of the plant without requiring an extensive root system. With one exception all the colonies visited by me grew on beaches characterized by rather coarse gravel set firmly in a matrix of sand, and covered over with a thin film of mud. The exception was found at my upper station on Gunpowder River, where a small but unusually luxuriant colony grew in a bed of sand. In this place the shore was protected from severe wave action by a zone of *Zizania aquatica* L., and I have no doubt that this circumstance alone made it possible for Isoetes to retain its hold at this place.

In Engelmann's manuscript notes, the following statement is accredited to William M. Canby: "I don't find any Isoetes (*riparia*, *Engelmanni*, *valida*, or *saccharata*) in pure mud or pure gravel; they always grow in mud which is deposited on gravel beds either by the tides (*riparia* and *saccharata*) or by rains which wash it down (*Engelmanni* and *valida*)."

d) *Isoetes saccharata* also requires that competition with other plants be slight. It is never found forming colonies of such density that it crowds itself, and its most frequent companion species have the same scattered habit. Only at my lower station on Gunpowder River have I found an exception to this. Here it is in competition with *Scirpus americanus* Pers. and is evidently suffering in the conflict. It would no doubt be entirely excluded by the Scirpus if the latter were as robust and densely set as is usual for that species on fresh water beaches.

When we consider the number of apparently essential elements in its habitat and the fewness and smallness of the areas in which all these elements are present, it is easy to understand the extreme localization of the species. But every restriction of habitat increases the difficulty of successful dispersal, and we may well ask how the species has succeeded in finding the places, often

so widely separated, which are adapted to its successful growth. Not only are difficulties presented by the requirements of its habitat, but there are factors in the life-history of *Isoetes saccharata* which are not favorable to rapid dissemination over wide areas. Heterospory is one of these. If spores are carried by any agency, microspores and megaspores must be lodged at the same place or the sporophyte itself must be carried. Besides, there seems to be a tendency in the species to dioecism,[12] and in proportion as this tendency is manifest the difficulties of dispersal are increased.

The means of dispersal upon which this and other species of like habitat may depend are several. The most important means must always be the water currents, because these are always acting at the time and place of spore production. Moreover, the chances are very good that the spores so carried may be lodged along some shore line where a new colony may be formed. In times of storm the waves may tear up whole plants from their anchorage in the littoral gravel and carry them far away to leave them finally stranded on some beach which may be adapted to the growth of the spores thus transported. Late last summer the writer saw a thrifty specimen of *Isoetes saccharata* floating in Chesapeake Bay, 100^{m} east of Stump's Point, at the mouth of Furnace Creek at the head of the bay, over 3^{km} from the nearest known station for the species, though possibly much nearer to some unknown station.

It is conceivable that biotic agencies might also occasionally serve as means of dispersal. Especially, from the observations of Charles Darwin and others, we might expect birds which frequent the shores to carry the spores occasionally on their feet or on their beaks, and as they move from one shore line to another, the spores so carried would be left in a new place favorable to growth. A. A. Eaton (*in litt.*) tells me that ducks are exceedingly fond of the spores of Isoetes, and that the lamellae of their beaks are especially fitted to retain them until washed

[12] PALMER, T. C., 1896, *loc. cit.* A. A. Eaton looks upon dioecism in this species as of rare occurrence, in which case it would be of slight importance in this connection.

out in another locality, and he thinks that this has been perhaps the efficient means of their dispersal.

A third possible method of dispersal is transportation of spores by the wind, but it is evident that successful dispersal by this means must be very rare. In the first place, the wind could only secure spores to carry after they had been stranded on the shore at high tide or in times of storm. Besides, the winds almost invariably blow across the shore line instead of parallel with it, so that the likelihood of the spores being stranded in a place adapted to their development is very slight indeed.

As the distribution of *Isoetes saccharata* appears to be limited by the confines of Chesapeake Bay, while the agency of birds and of the wind are not so limited, these agencies must be assumed to be relatively inefficient. For, if the waterfowl provided efficient means of dispersal, we should expect to find the species following the chief lines of migration as far as there were suitable habitats for its growth. As these lines of migration run parallel with the Atlantic coast, this would specially favor the transportation of *I. saccharata* into Delaware Bay and of *I. riparia* Engelm. into Chesapeake Bay. Our failure to find evidence of any such transportation is peculiarly striking when we bear in mind that the Back Creek station for *I. saccharata* is but little more than 16^{km} distant from the nearest point on Delaware Bay, while the known stations on Chesapeake Bay are in some instances separated by distances of more than 80^{km}.

We must conclude from these facts,[13] I think, that water currents supply the only efficient means of dispersal for this species, and that these have supplied the means by which new coloni[es] have sprung up in more or less distant areas. But even water currents could scarce be adequate to carry the spores from one

[13] This entire discussion is based on the assumption that *Isoetes saccharata* and *I. riparia* are really distinct species, as they have always been considered. In some of its forms *I. saccharata* approaches so nearly to *I. riparia* that the suggestion is not far that they are ecological varieties of the same species. Too little is known, as yet, about ecological varieties, to make more than a suggestion permissible. It is obvious that successful transportation from the one bay to the other may have taken place any number of times, if in each case the ecological conditions were such as to produce from the spores of a single specimen, *I. riparia* in Delaware Bay and *I saccharata* in Chesapeake Bay.

station to the mouth of the river in which it occurs, thence up or down the coast to a neighboring river, and up that river to the fresh-water portion near the head of tide water. Such a transportation, if at all possible, must depend upon the most exceptional of circumstances.

Probably a truer explanation is found in relation to the geological history of the bay. It is believed by some geologists[14] that the region about Chesapeake Bay is now sinking, and it is certain that it has recently sunk after a period of elevation. In fact, it seems to have been elevated and depressed several times in its Pleistocene history.[15]

The position of old shore lines with their sea cliffs and terraces gives evidence of the amount of subsidence of the land at each period of sinking, but no evidences remain as to the height to which the land rose during each period of elevation. The present elevation of the land is such that the water of the bay is fresh to Spesutie Island, about ten kilometers below the mouth of the Susquehanna River. During periods of greater elevation the water was fresh further to the south. When the land was so elevated that the water was fresh at the mouth of the Potomac River, favorable habitats along the shore of the bay must have been occupied by the progenitors of the *Isoetes saccharata* colonies which now occur in the upper estuarine portion of the tributary rivers. As the land sank and the rivers were ponded farther and farther from their mouths, new areas became adapted to the growth of Isoetes, and new colonies were formed. Simultaneously the colonies furthest down stream were destroyed by the advance of salt water. In this way there came to be, instead of a single colony or group of colonies at the head of Chesapeake Bay, as many distinct colonies as there were ponded tributaries. So long as the land continued to sink, the successful reproduction was on the up-stream side, and destruction followed *pari passu* on the down-stream side until the present condition of widely separated colonies was brought about. In periods of

[14] COOK, GEORGE H., Geology of N. J. 1868: 343 *et seq.*

[15] MCGEE, W J, Am. Jour. Sci. **35**: 463–466. 1888. DARTON, N. H., Bull. Geol. Soc. Am. **2**: 450. Ap 1891. SHATTUCK, GEORGE B., Am. Geol. **28**: 100–105. Ag 1901.

elevation, the reverse process must have taken place, and the many distinct areas must have been merged again into one. This may have taken place as often as the bay has been up and down, and certainly has happened as often as the bay has risen and fallen since *Isoetes saccharata* entered it.

Just how or when Isoetes entered Chesapeake Bay is, of course, impossible to say, except that, according to this hypothesis of its dispersal, it must have been introduced before the last sinking of the coastal plain.

From what has been said of the requirements of its habitat and the means of dispersal of Isoetes, it will be seen that the barriers between Chesapeake Bay and Delaware Bay and between both of these and other fresh tidal waters, are of such definite character as to render these bays virtually islands of water in oceans of land. As we find *Isoetes saccharata* nowhere else than in Chesapeake Bay and *Isoetes riparia* nowhere else than in Delaware Bay, it seems fair to assume that neither of these species ever existed as such outside of the body of water to which it is now limited, and that we have here examples of initial endemism entirely comparable with that so common upon oceanic islands.

These two species are closely related and probably stand to each other in relation of parent and offspring; but which is the parent and which the offspring may not be easy to decide. Or perhaps they were the offspring of a common parent different from both. The nearness of this relationship was emphasized in the recognition of the two varieties, *Isoetes saccharata Palmeri* A. A. Eaton and *I. saccharata reticulata* A. A. Eaton, both possessing characters intermediate between *Isoetes saccharata* Engelm. and *Isoetes riparia* Engelm. The significance of these forms will be increased rather than lessened if they should prove to be untenable as varieties. For if these varieties are shown to be simply stages in the development of a polymorphic species, the greater range of variability which must then be admitted as a character of *I. saccharata* Engelm., coupled with the fact that those variations in several different features are in the direction of *Isoetes riparia* Engelm., would make almost certain the inference that an extreme variation of *I. saccharata* had become somewhat fixed through its isolation in Delaware Bay.

Careful cultures will be necessary to demonstrate conclusively the polymorphism of *Isoetes saccharata* Engelm., but that seems at present the most satisfactory explanation of the following facts. My attention was called both by A. A. Eaton and T. C. Palmer to several futile attempts which had been made to secure *typical* material from the *type* locality. It appears that the original description was written from a form which is of very rare occurrence. Even the co-type material did not agree with the type, and the Wicomico station has been visited several times since, but no typical material has been secured there. The infrequency of the recurrence of the typical form is well shown by the fact that my collection from Hunting Creek, Va., appears to be the first material collected since 1863, which agrees in its spore characters with the type material. The striking fact here is that my collection of typical *I. saccharata* Engelm. came from the type locality of variety *reticulata* A. A. Eaton. This colony is only a few square meters in extent and a considerable number of specimens had been collected there by Vasey and Coville in 1888, and by W. R. Maxon in 1900 and 1901. Every one of those specimens appear to have been var. *reticulata.* I collected at the same place perhaps a dozen specimens, every one of which was typical *I. saccharata.* The only plausible explanation of these facts, it seems to me, is that the identical plants which had been var. *reticulata* at the time of the previous collections, were last year typical *I. saccharata.*

Another similar circumstance which lends support to this explanation is that E. S. Steele's collection at Four Mile Run in 1899 was nearly typical *I. saccharata,* whereas the considerable number of specimens secured by me in 1902 from the same spot, all showed extremely well-marked characters of var. *reticulata* A. A. Eaton.

I have no such striking facts against the validity of var. *Palmeri* A. A. Eaton, since I visited no *Palmeri* station, but much of my material from the head of the bay was intermediate between *I. saccharata* and var. *Palmeri,* as was also Coville's Mount Vernon collection. T. C. Palmer found the same conditions at Cabin Johns Creek and Town Point in Elk River. If

Isoetes saccharata should prove to be polymorphic, as these facts suggest, the result will be of interest in its bearing upon such species as *I. echinospora* Durieu and *I. velata* A. Br., whose numerous intergrading forms have proved so baffling to systematists.

By way of summary, then, *Isoetes saccharata* Engelm. has been located in a number of tributaries of Chesapeake Bay from the the Potomac and Wicomico Rivers to the head of the bay.

The species is conceived to be autochthonous in Chesapeake Bay, and to bear toward *Isoetes riparia* Engelm. the relation of parent to offspring.

Its present distribution is explained by the geomorphic movements of the coastal plain.

Certain facts are presented which suggest that the species is polymorphic, and that the varieties *Palmeri* A. A. Eaton and *reticulata* A. A. Eaton are untenable.

I take pleasure in acknowledging my indebtedness to Wm. M. Canby, F. V. Coville, T. C. Palmer, E. S. Steele, and W. R. Maxon for notes on their several collections of *Isoetes saccharata* Engelm. and its forms; to Dr. J. N. Rose for data from U. S. National Herbarium, and Dr. Wm. Trelease for data from the Herbarium of the Missouri Botanical Gardens, and from G. Engelmann's manuscript notes; also to Miss Veva M. Brower for notes on the Nanticoke River at Seaford, Del. But I am under special obligations to A. A. Eaton, who has kindly examined all my material and has encouraged me with suggestions and criticisms on the discussions involved in this paper. To all of these I wish to express my sincere thanks.

THE UNIVERSITY OF CHICAGO.

A SKETCH OF THE FLORA OF SOUTHERN CALIFORNIA.

S. B. PARISH.

THE name "Southern California" is here restricted to a territory somewhat less extensive than that to which it is sometimes applied; but even as here limited, to the five southernmost counties—Los Angeles, San Bernardino, Riverside, Orange, and San Diego—it includes one quarter of the area of the whole state, and exceeds in size the great state of Ohio. It has an area of 40,889 square miles (over 100,000 sq. kilometers). Its greatest breadth, from north to south, is 210 miles (336^{km}), and from east to west 282 miles (451^{km}). It lies between 32° 30′ and 35° 40′ north latitude, and between 37° 15′ and 42° longitude west from the meridian of Washington. Its western boundary is formed, for the greater part, by the Pacific Ocean, but partly by the counties of Ventura and Kern, and these two counties, together with Inyo, bound it on the north, while for a short distance on the northeast it touches the state of Nevada. The river Colorado separates it on the east from Arizona, and on the south it adjoins the Mexican state of Lower California.

Before proceeding to a consideration of the flora of this region it is desirable to speak briefly of the physical character of its surface, and of its climate, since these are the most important influences by which the development and distribution of its plant population have been determined.

OROGRAPHICAL FEATURES.

The region is one of mountains, whose ramifications embrace numerous valleys of greater or less extent. The main axis of upheaval is a continuation of the Sierra Nevada. It enters our region at Ft. Tejon, in which neighborhood the Coast Range unites with it; and it extends in a course from northeast to southwest, culminating in the twin summits of San Bernardino and Grayback, respectively $10{,}100^{ft}$ ($3{,}080^{m}$) and $11{,}725^{ft}$

(3,575 ^{m}) above sea level. The mountains between these limits are generally called the San Bernardino Range.[1] It is made up of the Sierra Liebre and Sierra Pelona, between Tejon and Soledad Passes; the San Gabriel Mountains, with the peaks of San Gabriel, 6,232 ^{ft} (1,900 ^{m}), San Antonio, 10,120 ^{ft} (3,085 ^{m}), and Cucamonga,[2] 6,500 ^{ft} (1,980 ^{m}), between Soledad and Cajon Passes; and the San Bernardino Mountains proper, between Cajon and San Gorgonio Passes.

North of Soledad Pass the mountains are comparatively low, but rugged and broken. An important cross range, the Santa Monica, maintaining an altitude of 2,000 to 3,000 ^{ft} (600–900 ^{m}), stretches from San Fernando Peak, 3,793 ^{ft} (1,156 ^{m}), to the Pacific Ocean at Point Duma. But south of Soledad the mountains become higher, towering up abruptly, from a valley base 500 to 1,000 ^{ft} (150–300 ^{m}) above the sea, to a ridge line having an altitude of 5,000 to 6,000 ^{ft} (1,500–1,800 ^{m}). From the desert they present a less lofty appearance, since on that side the base altitude is 3,000 to 3,500 ^{ft} (900–1,066 ^{m}).

Grayback throws out an important spur, in the direction of the main range, towards the Colorado River. This may be known as the Chuckawalla Range, although that name is often restricted to its further extremity. It separates the Colorado and the Mojave[3] Deserts.

The low San Gorgonio Pass separates Grayback from San Jacinto Mountain 10,805 ^{ft} (3,993 ^{m}), an air-line distance of some twenty miles. The mountains here spread out, their course changes, and is less defined. But regarding the line which divides the watershed draining into the Pacific from that which drains into the desert, its direction is found to be about 10°

[1] First by Blake in Pac. R. R. Rep. 5. He also suggested the name "Peninsular Range" for the mountains extending from San Jacinto into Lower California, but this name, although appropriate, has failed to find acceptance.

[2] This was a troublesome name to the early explorers. It is Quiqual Gungo of Pac. R. R. Rep. 4 : 38; Quiquai-mungo *ibid.* 5^2 : 80; and Kikal Mungo *ibid.* 7 : 8.

[3] I use the spelling long current in California. While only the Spanish orthography of an aboriginal name, it harmonizes with such Spanish names of the region as Tejon, Cajon, etc. The U. S. Board on Geographical Names has adopted the form "Mohave," but this should not be allowed to supersede a well-established local usage. The name was first printed by Fremont in 1844, who spelled it "Mohahve."

south of east. Here it is the desert face which is precipitous, its base, for the most part, not exceeding 500 ft (150 m) above sea level, while upon the other side San Jacinto overlooks a confusion of ridges and lesser peaks.

A main cross-range from San Jacinto parallels the San Bernardino Mountains at a distance of about forty miles. It comprises the Palomar Mountains[4] (summit 5,800 ft, 1,765 m) and the Temescal Mountains, whose terminal summit, Santiago Peak,[5] has an altitude of 5,675 ft (1730 m), and separates the San Jacinto Valley from the coast region.

Further south Cuyamaca Mountain, 6,500 ft (1,980 m) high, dominates a rugged region of high ridges and narrow valleys. In default of a better name the entire chain, from Tejon Pass to Cuyamaca, may be called the Nevadan Range, since it is, in truth, a part or a continuation of the Sierra Nevada.

THE DESERTS.

The topography of the desert region is less accurately known. It comprises two distinct divisions: the Colorado Desert and the Mojave Desert. The former, stretching southeastward from San Gorgonio Pass to the Mexican boundary, is a great valley, 180 miles (288 km) long, and 30 to 50 miles (50–80 km) wide. In its center it sinks into a deep depression over 250 ft (76 m) below sea level,[6] the dry bed of what has been in prehistoric times first an arm of the sea, and later a fresh or brackish lake. In this depressed area, and notably near Salton, volcanic forces yet manifest themselves in "mud volcanoes" and extensive solfataras.

The lower part of this desert, toward Yuma, and in the New River region, consists largely of pebble-covered clay plains and

[4] Also known as Smith Mountains.

[5] Sometimes called Saddleback, or Santa Ana peak. In 1861 Dr. Whitney gave it the name Mt. Downey, which fortunately has never been accepted. This whole range is often called the Coast Range, but it has no connection with the true Coast Range of California.

[6] The following are the altitudes in feet at stations on the Southern Pacific Railway where it crosses this depression: Seven Palms, 582; Indio, —20; Walters, —195; Dos Palmas, —253; Salton, —263; Flowing Well, 5; Tortuga, 185. The total distance, in a straight line, is about 80 miles (130 km).

shifting sand hills, and has an altitude of 150 to 400 ft (45–120 m). The area of the Colorado Desert has been estimated at 9,000 square miles (14,400 sq km).[7]

The Mojave Desert lies on the north side of the San Bernardino Range, and its continuing spur, the Chuckawalla Mountains; eastward it stretches to the Colorado River, and northerly to and beyond our boundary lines. Its greatest length, east and west, measured in an air-line, from Gormans Station, at the head of Antelope Valley, to the Needles on the Colorado River, is about 130 miles (210 km). Its width, north and south, from the mountains which form its southern rim to our northern boundary, varies from 30 to 60 miles (48–96 km). No estimate of its area appears to have been made. Within our limits its altitude is much greater than that of the Colorado Desert, being 2,000 to 3,500 ft (660–1,067 m), but beyond them it also sinks, in Death Valley, below sea level.

Its whole surface is cut up by short isolated ranges and "lone mountains," which are surrounded by sloping mesas, or enclose basins whose lowest portions are occupied by "dry lakes." Some of these are level expanses of hard, elastic clay, smooth and bare as a racetrack, and bordered by a narrow belt of nitrophilous vegetation. Receiving the scanty storm water that rolls down from the bare hills about them, they at times may be transformed into tenacious mud, or even be covered by a few inches of water. Or the floor of these basins may consist of what prospectors call "self-rising soil," a deep bed of loose alkaline powder, slightly crusted over, into which foot and wheel sink wearily; or, again, it may be covered with a snowy incrustation of soda salts.

The highest mountain of the Mojave Desert is Ivawatch, 6,290 ft (1,917 m), on the northern boundary of San Bernardino county. Some twenty miles southwest is Pilot Knob, 5,525 ft (1,684 m), a noted landmark, as its name indicates. Mt. Manchester, near the Needles, is 4,570 ft (1,448 m) high. But the most important of these ranges are the Providence Mountains,

[7] This is for the part of it within the United States; beyond the boundary it continues to the Colorado River and the head of the Gulf of California. Its width on the Colorado River is fully 75 miles (120 km).

situated on the eastern border of the desert, and extending some 75 miles (120^{km}) in a NNE and SSW course, culminating at the south in Mt. Edgar, $6,350^{ft}$ ($1,935^{m}$).

DRAINAGE SYSTEMS.

A country such as I have described, if in a region of abundant rainfall, would abound in limpid lakes, and in living streams, some of which would be of considerable volume. But far other is the case under the arid conditions which here exist. Even the streams rising in the high mountains of the San Bernardino range are infrequent, slender and inconstant; and of still less importance are those which drain the mountains to the south. In seasons of unusual precipitation they become raging torrents, and at such times the larger streams may carry their waters to the sea; but ordinarily their volume is insufficient to reach their nominal mouths, while in summer they dwindle down to thin rivulets which repeatedly sink and reappear in their wide sandy beds.

The San Gabriel Mountains give rise on their desert slopes to Rock Creek,[8] which ventures beyond their base only in wet weather. On their seaward side they are drained on the west by the Los Angeles and San Gabriel Rivers, and on the east by Lytle Creek, a tributary of the Santa Ana.

The San Bernardino Mountains furnish the waters of the most important streams of the whole region. On the northern watershed the Mojave River has its source in Holcomb Valley, at an altitude of $7,000^{ft}$ ($2,134^{m}$). It flows 75 miles (120^{km}) in a northerly direction, and then turning to the east continues for 60 miles (96^{km}) further, the distances being measured in an air line, but following its meanderings its length is fully 200 miles (320^{km}). In its course it disappears eight times in its sandy channel, leaving it entirely dry for long intervals, and is finally lost in Soda Lake (alt. $1,116^{ft}$, 340^{km}), a flat, elliptical depression some 70 square miles ($112^{sq\,km}$) in area, occasionally flooded a few inches deep with water, but usually whitened with alkaline efflorescences. The eastern drainage of these mountains forms

[8] This is the "Johnson's River," of Blake, Pac. R. R. Rep. 5:30 *et seq.*

the Arroyo Blanco, or Whitewater, a strong stream which is soon lost in the sands of the Colorado Desert.

The Santa Ana River carries the seaward drainage, and has an airline course of 85 miles (136^{km}), in a southwest direction, to the ocean, which, it is said, its waters have been known to reach in high floods. In ordinary stages it sinks soon after disemboguing from the mountains, and reappearing after ten miles (16^{km}) carries more or less water nearly to Santa Ana.

San Jacinto Mountain gives rise to a stream bearing the same name, which follows a southwest course to Elsinore Lake. Its channel, however, is only intermittently supplied with surface water. The Santa Margarita, the San Luis Rey, the Sweetwater, and some lesser streams, drain the mountains of San Diego county, and have a character similar to those already described.

The Colorado River, which touches the border of the state, does not receive from it a single tributary, great or small; but an abandoned channel, the so-called New River, carries the waters of the Colorado, in times of great floods, into the southeastern part of the desert and to the Salton Sea.

GEOLOGICAL FORMATIONS.

The great mountain axis consists principally of granitic formations, and such is the prevailing character of the subordinate ranges. There are occasional outcroppings of limestones, but always of limited area. A range of Tertiary hills, conglomerates, sandstones and shales, beginning near Pasadena, stretches to the Santa Ana River, where it is divided by the granites of the Temescal Mountains, a narrow arm continuing along their northeastern base, while a wider one (10–18 miles, $16–29^{km}$) turns toward the coast, which it reaches at San Juan, and follows it thence to the Mexican boundary. A less important Tertiary formation skirts the southern base of the San Bernardino Mountains from Santa Ana Cañon to the Whitewater, occupying an area of 30 miles (48^{km}) in length by 1 to 5 miles ($1.6–8^{km}$) in width. The same formation also appears in the Palos Verdes hills, and on the islands off the coast.

The San Fernando Plains, the wide expanse of fertile country

between Los Angeles and Santa Ana, the San Bernardino, San Jacinto, and many smaller valleys are Quaternary and Recent. They include sandy and gravelly mesas, as well as rich loams, ferruginous clays, and black adobe. Almost without exception they contain soda salts, from the small percentage which increases fertility, to the excess which forbids the growth of all but a few specialized plants. Recent formations also prevail throughout the Colorado Desert.

The formations of the Mojave Desert are less well known. The mountains are, for the most part, granitic, the intervening mesas and valleys being of recent deposition. Evidences of former volcanic activity are exhibited in places. This is most marked in the country between Point of Rocks and Bagdad, on the Santa Fé Railway, an air-line distance of some 80 miles (130^{km}). Here the rocks are metamorphosed, and often display commingled bands and patches of reds, blues, greens, purples and yellows.[9] The mesas are strewn with scoria, the hills have black lava caps, fissure lines are seen, and lava streams may be traced for miles. Not less than a dozen volcanic cones are known in this region. One of the largest is 450^{ft} (137^{m}) high and $3{,}000^{ft}$ (914^{m}) in diameter at base; the extinct crater at the summit is 750^{ft} (228^{m}) in diameter and 150^{ft} (45^{m}) deep. The Providence Mountains limit this volcanic area on the east, but northward other less known centers exist.

CLIMATIC CHARACTERISTICS.

Southern California possesses a variety of climates, but throughout the larger part of it aridity and high temperature are the dominant features. There are few, if any, absolutely frostless localities, but there are many where only light frosts ever occur, and which may be quite untouched for several successive years. At altitudes below $1{,}500^{ft}$ (457^{m}) the midwinter temperature rarely falls below $25°$ F. ($-4°$ C.), and the same altitude marks the ordinary limit of even light snowfalls.

But ascending to higher altitudes a different climate and a cooler temperature is soon reached. Thus at San Bernardino

[9] This peculiar coloration gave the Calico Mountains their prosaic name, in reference to their variegated tints.

(1,075 ft, 328 m) in the five years 1895–9 the highest point reached by the thermometer was 110° F. (43° C.) and the lowest 23° F. (– 5° C.).[10] At Little Bear Valley, 5,150 ft (1,569 m), in the adjacent mountains, distant about 12 miles (20 km) in an air line, the extremes during the same years were 93° and –2° F. (34 and – 19 C.).[10a] That is, a temperature was reached in summer in the valley 17° above that of the mountain, while the winter temperature lacked 21° of falling so low. At Big Bear Valley, 6,500 ft (1,981 m) a temperature of –14° F. (–25.5° C.) has been observed,[11] frosts occur in midsummer, and ice sometimes forms on an August night. No observations have been made at greater altitudes, but it is evident that at 10,000 or 12,000 ft (3,000–3,600 m) very low temperatures must be reached. These lofty summits are white in the winter months, and on their northern slopes the snow fields often linger late into summer. After a winter of unusual accumulations some shrunken remains may even persist into a second season.[12] Even at altitudes as low as 6,000–7,000 ft (1,830–2,130 m) there are sheltered cañons where snow banks yet linger at midsummer.

Contrary to common opinion, recorded observations establish the fact that lower temperatures are reached at stations in the desert region than at places having the same altitude on the seaward side of the mountains.[13] A great difference is shown also at the other extremity of the scale. The highest temperatures recorded on the coast are 85°–100° F. (30–38° C.); further back from the sea 100°–112° F. (38–44° C.) is reached; but at stations in the deserts records of 115°–128° F. (46–53° C.) have been made.[14]

The annual precipitation is very unequal in amount, not only in the different regions, but in the same region in different years. As an example of yearly variability the rainfall at Los Angeles

[10] From the Records of Dr. A. K. Johnson.

[10a] Records of Arrowhead Reservoir Co.

[11] Records of the Bear Valley Co.

[12] Mean annual snowfall at Little Bear Valley 1895–9, 73 in (1,854 mm); greatest single snowfall, 39 in (990 mm). Records of Arrowhead Reservoir Co.

[13] At Victor, in the Mojave Desert, altitude 2,713 ft (828 m) killing frosts occur in August.

[14] At Mammoth Tank, July, 1887, 128° F.; July, 1884, 126° F.

of 32.25 in (819 mm) in 1869 may be compared with that of 4.83 in (122 mm) in 1898. In the desert region the rainfall is always very small, and in average seasons is greatly exceeded by that of the cismontane region, but years of extreme drought have occurred in which the difference was less marked.

The appended table exhibits the normal amount of precipitation at places whose records extend over a period of more than fifteen years. The average for the three intramontane stations is 14.95 in (380 mm), or about five times that of the desert station.

NORMAL PRECIPITATION.

Stations	Altitude		Years of Record	Monthly Precipitation				Yearly Precipitation	
				Least		Greatest			
	Feet	Meters		In.	Mm.	In.	Mm.	In.	Mm.
Los Angeles	270	84.1	21	T	T	4.0	102	18.1	460
San Diego	12	3.6	42	0.1	2.5	2.1	53	9.8	249
San Bernardino ..	1,075	327.6	29	0.3	7.6	3.6	91	17.0	432
Yuma	140	42.7	16	T	T	0.6	15	3.2	77

Nearly as great a disparity exists between the rainfall of the intramontane and the Nevadan regions, but data from the latter are few and not easily obtained. A partial means of comparison is afforded by the following table. The seasons are from July to June. The distance of the two stations in an air-line is about 12 miles (20 km); the difference of altitude is 4,075 ft (1,242 m).

PRECIPITATION FOR SIX SEASONS, 1893–94 TO 1898–99.

Stations	Altitude		Precipitation					
			Greatest		Least		Mean	
	Feet	Meters	In.	Mm.	In.	Mm.	In.	Mm.
San Bernardino[14]	1,075	328	20.98	533	7.49	190	11.61	295
Little Bear Valley[15]	5,150	1,570	60.61	1,542	19.79	502	33.08	840

The rainfall at the mountain station is nearly three times

[14] Dr. A. K. Johnson's record. [15] Arrowhead Reservoir Co.'s record.

that of the subjacent valley. The seasons of greatest and least rainfall were synchronous.

But for the purposes of the present inquiry the extreme of moisture and drought to which plant life is exposed is of as great importance as the average amount of rainfall; and the distribution in time of this amount is a factor of equal value. Again it will be found that in these respects the desert vegetation is at a disadvantage. Throughout the deserts total yearly rainfalls of 1.5 to 4 ^{in} (38–101 ^{mm}) are the rule, and at some stations a whole year may pass with absolutely no measurable precipitation. But this small amount is so evenly distributed through the year as to produce much less effect, certainly for annual plants, than if it were concentrated in a few months. The table below shows the normal distribution of rainfall throughout the year at two desert stations, compared with that at two stations on the coast.

NORMAL MONTHLY PRECIPITATION IN INCHES.

Stations	Years	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Keeler	8	0.2	0.4	0.2	0.3	0.4	0.2	0.1	0.2	0.3	0.3	0.4	0.4	3.3
Yuma	16	0.4	0.6	0.2	0.1	T	T	0.1	0.4	0.1	0.3	0.3	0.6	3.2
San Diego	42	1.6	2.1	1.0	1.0	0.3	0.1	0.1	0.1	0.1	0.3	1.0	2.1	9.8
Los Angeles	21	3.9	4.0	2.2	1.3	0.3	0.1	T	0.1	T	0.7	1.6	3.7	18.1

It here appears that the scanty rainfall of the desert stations is quite evenly distributed through the whole year, while at San Diego 9.1 inches out of the total 9.8 inches, and at Los Angeles 17 inches out of 18.1 inches fell during the growing season between November and May. That is, over 95 per cent. of the total rainfall at these places comes at a time when, owing to a lower temperature and a more declined sun, it is not subject to rapid evaporation, and avails most for the growth of vegetation. On the other hand almost all the desert rainfall may be regarded as ineffective by reason of its equal distribution.

It must be remembered, however, that all our recorded observations were made at stations in the open deserts, whereas had they been made in the cañons of the circumscribing mountains, somewhat more favorable results would have been obtained.

The rainclouds hug the mountains, and in winter one often may pass from the bright sunshine of the desert valleys through mist and drizzle to heavy showers by ascending for a few miles some cañon leading up the mountains. Hence it is in the cañons that the botanist learns to expect the most abundant and varied vegetation.

The desert mountains are also the scenes in midsummer of "cloud-bursts," or violent thunderstorms. These discharge in a short period and over a limited area a great quantity of water, and for a few hours the parched cañons are filled with rushing torrents. I have found a measurement of but one of these "cloud-bursts," and that only partial. At Campo on a day in August, 1891, there fell in such a storm 16^{in} (406^{mm}) of rain, before the gauge was washed away, preventing a complete measurement.

On the seacoast the aridity of the atmosphere is modified by frequent fogs and damp air-currents from the sea; and these ameliorating influences extend their benefits, in a less degree, inland, but do not pass beyond the mountains to modify the dryness of the desert air, while the strong winds almost constantly blowing there, produce a further desiccating effect.

PHYTOGEOGRAPHICAL AREAS.

It will readily be understood, from the preceding account, that the region under consideration consists of three divisions, differing from one another in both topography and climate. Consequently each of these will be found to possess a distinct and characteristic flora, and to constitute a separate life area.

In its relation to the biological divisions proposed by Dr. Merriam[16] the entire territory may be regarded as a part of the Sonoran province, in the midst of which arise two isolated peaks belonging to the Boreal province. A scanty Arctic flora occupies the summits of these peaks, and beneath it a diligent study can disentangle the Hudsonian and Canadian zones. This has been worked out very carefully and thoroughly by Mr. H. M. Hall,[17]

[16] MERRIAM, J. HART, N. Am. Fauna 3:20, map 5; National Geo. Mag. **6**:229; Yearbook U. S. Dept. Agr. **1897**:203.

[17] HALL, HARVEY M., A botanical survey of San Jacinto Mountain. Univ. of Cal. Pub. Bot. **1**:1–144.

for San Jacinto, one of these mountains; the other, San Bernardino, yet awaits such detailed study.

But as might be expected from the position of the mountain chain, narrow and between two hot and arid districts, the zonal differentiation is not here carried out to the extent, or with the distinctness, that is exhibited in mountains more favorably situated, and of greater area. Indeed, the commingling of the Hudsonian and Canadian with the Neutral (*Pinus ponderosa*) belt is a marked feature of these mountains.

While, therefore, in a detailed study the separation of these zones may be preserved advantageously, it is more convenient for the purposes of a general view to unite the whole pine belt, which I propose to do under the name of the Nevadan area.

Above it the Arctic flora is feebly represented; and by it the remaining territory is divided into two life-areas. The Desert area comprises the deserts north and east of the Nevadan Range; the district between that range and the sea may be designated as the Cismontane area.[18] It remains to consider the character and limits of these several divisions, and of their subdivisions.

THE ARCTIC-ALPINE ZONE.

As has been stated already this zone is represented only on the summits of the two highest mountains, Grayback and San Jacinto. And it is but the scanty vestiges of an Arctic flora that lingers on these lofty summits, much scantier than their altitudes would justify one in expecting, even taking into consideration that this is the southern known limit of the Arctic flora on the North American continent. The summit of Grayback is flat and consists of porous decomposed granite, unfavorable to the growth of plants. San Jacinto is more fortunate, having on its precipitous northern face some steep, shaded cañons, preserving perpetual snows. But for all that, it does not exceed in species its less favored neighbor. A single species, *Ranunculus Eschscholtzii*, has been found on both peaks, *Arenaria hirta verna* and *Antennaria alpina* have been collected on Grayback, while from San Jacinto *Carex Preslii* and *Oxyria digyna*

[18] This has been designated usually as the Intramontane area, but the present term seems preferable.

have been added to the short list. Further explorations may be expected to increase it, but not greatly.

THE NEVADAN AREA.

The lower limit of this area coincides with that of *Pinus ponderosa*. On cismontane slopes this is seldom below 5,000^{ft} (1,524^{m}) altitude; but on the opposite side the influences of the desert force it up to 6,000^{ft} (1,828^{m}), and even to 7,000^{ft} (2,133^{m}) above sea level. This region contains the only real forests in the entire territory, and while these are far inferior to those in the damper and cooler parts of the Pacific Coast, they are by no means insignificant, either in extent, or in the size and variety of the trees which compose them.

As already stated the zones which I have included in this area are much confused. Perhaps the best marked is the Hudsonian, which we may consider as indicated by the presence of *Pinus flexilis*. This is known to occur on Grayback, San Jacinto, and Santa Rosa peaks, and it should be found on one or two other high summits. As a zonal index its proper limit would be between 9,000 or 10,000 to 12,000^{ft} (2,750–3,650^{m}). But under favorable conditions it descends 1,000–2,000^{ft} (300–600^{m}) lower into the Canadian, and in at least one instance an isolated Hudsonian "island" occurs at 6,500^{ft} (1980^{m}), well down in the Neutral or Transition zone.[19]

The Canadian zone, which may be taken as indicated by *Pinus Murrayana*, is even less definitely marked. This pine is not uncommon in places as low as 6,500^{ft} (1,980^{m}), but it is better developed in moist valleys 1,000–2,000^{ft} (300–600^{m}) higher, and becomes more abundant as one ascends, until it mingles with the limber pine of the superior zone.

But the most important zone is the Neutral, or Transition; and it is the only one represented in the greater part of the Nevadan area. The principal tree throughout this zone is *Pinus ponderosa*. Its lower limits have been specified, and its upper limit may be placed at 8,500^{ft} (2,590^{m}), or occasionally, and under favoring conditions 500–1,000^{ft} (150–300^{m}) higher.

[19] For an account of this see "The Flora of Snow Cañon, California," by the writer, in Plant World 4:227.

With this species is intermixed a considerable proportion of *Abies concolor*, *Libocedrus decurrens*, *Pinus Lambertiana* and some *P. ponderosa Jeffreyi*, without zonal differentiation, except that the Abies is more abundant and of greater size toward the upper limit, at 7,500–8,000^{ft} altitude (2,286–2,438^{m}).

On each slope of the mountain there is, beneath the Pine or Neutral zone, an intermediate, or true Transitional zone. The one differs entirely from the other, each possessing plants peculiar to itself and also representatives of the superior and the inferior zones. On the desert side this zone is nearly crowded out, and is present only in a narrow strip, between 6,500 and 7,500^{ft} (1,980–2,286^{m}) altitude, along the northern slope of the San Bernardino Mountains, and reaching from Bear Valley some fifteen miles towards Cajon Pass. It is indicated by an abundant growth of *Juniperus Californicus* and *Cercocarpus ledifolius*. It is much intruded upon by the plants of the zones above and below it, and within its limits may be seen in juxtaposition such incongruous species as *Pinus ponderosa* and *P. monophylla*, *Abies concolor* and *Yucca brevifolia*.

Of this transitional character, also, is the belt of *Pseudotsuga macrocarpa* and *Pinus Coulteri*, extending along the cismontane flank of the Nevadan Range, at 3,000–4,500^{ft} (915–1,370^{m}) altitude. The former is more abundant at the northern part of the belt, and the latter at the south, where it occupies a position similar to that of the closely allied *P. Sabiana* in the foothills of central California. To the north *Pinus Coulteri* is commoner on the lower ridges within the *P. ponderosa* zone.

The following table shows those genera which, in our territory, are found only in the Nevadan area.[20] Genera which are abundant and widely distributed are in SMALL CAPITALS; those local and rare in *italic*.

[20] In this, and in subsequent tables of regional distribution those genera are omitted which are represented by endemic species only. Want of space prevents an extension of this investigation to the species of such genera as have representatives in more than one area, but its extension to these would be found to reinforce the conclusions reached. In determining the sources, or geographical affinities, of the elements composing the floras of the different areas, regard is had, not to the distribution of the genus as a whole, but of the particular species under consideration.

GENERA FOUND ONLY IN THE NEVADAN AREA.

Exclusively Nevadan		Boreal	
LIBOCEDRUS	Heracleum	Athyrium	Pterospora
Danthonia	*Pyrola*	*Woodsia*	Geum
Hemicarpha	*Chimaphila*	CYSTOPTERIS	HYPERICUM
VERATRUM	SARCODES	*Cryptogramma*	Circæa
Iris	Rhododendron	ABIES	Hippurus
Corallorhiza	*Brianthus*	Alopecurus	Myriophyllum
CASTANOPSIS	*Cycladenia*	Glyceria	Gentiana
SPRAGUEA	*Boschniakia*	Puccinella	*Polemonium*
Lewisia	KELLOGGIA	*Trisetum*	Lappula
Heuchera	Hemizonella	Luzula	Taraxacum
Philadelphus	Hulsea	Smilacina	Crepis
Heterogaura	*Raillardella*	Actæa	Hymenopappus
Sphænosciadium		BARBAREA	Arnica

In the first two columns are placed those genera which, as to the species by which they are here represented, belong exclusively to the flora of the Sierra Nevada; in the last two those which have a more or less wide distribution throughout the whole Boreal province. But it is to be noted that every genus, without exception, has for its representatives in our flora the identical species which are found in the more northern parts of the Sierra Nevada. Moreover, with the exception of eight of the Nevadan genera and three of those of wider distribution,[21] all belong in the so-called Neutral or Transition zone.

From a consideration of this table it is evident that the flora of these southern mountains coincides with that of the general Sierra Nevada, of which it is physiographically a part. And so far as its position in the phytogeography of North America is indicated by distinctive genera, the Transition zone is preponderately Boreal rather than Sonoran.

THE DESERT AREA.

The Desert area consists of two very distinct subareas: the Mojave subarea, which includes all the country to the north and east of the San Bernardino and Chuckawalla Mountains; and the Colorado subarea, which consists of the great desert valley between the Chuckawalla Mountains and the southern prolonga-

[21] Namely: *Castanopsis, Philadelphus, Pyrola, Chimaphila, Bryanthus, Cycladenia, Boschniakia, Raillardella, Athyrium, Woodsia, Cryptogramma.*

tion of the main range. These are locally known as the Mojave and the Colorado Deserts.[22] These two subareas have many plants which are common to both, but each possesses also a distinctive flora. These characteristics, so far as they relate to genera, are exhibited in the subjoined table.

GENERA PECULIAR TO THE DESERT AREA.

Colorado Subarea	Mojave Subarea	Both Subareas
Northeastern Element	Northeastern Element	Northeastern Element
Astephanus	_Actinella_	Anisocoma
	Amsonia	Grayia
Southeastern Element	Atrichoseris	Piptocalyx
	*Bouteloua	_Tricardia_
WEDELIA	Cleomella	
*Argythamnia	*EUROTIA	Southeastern Element
Ayenia	_Forestiera_	
*Beloperone	Glossopetalon	Acamptopappus
Boerhaavia	Glyptopleura	Achyronichia
*_Calliandra_	KOCHIA	Baileya
*Cercidium	LYGODESMIA	Bernardia
Chloris	Monoptilon	Cladothrix
*_Condalia_	Phellopterus	HILARIA
Dicoria	PURSHIA	*KRAMERIA
*Fagonia	STANLEYA	*LARREA
Fouquiera	*Salazaria	Mohavia
*Hibiscus	*Syntrichopappus	Nolina
*Horsfordia		THAMNOSMA
*Hoffmanseggia		Trichoptilium
*HOFMEISTERIA		
*HYPTIS	Southeastern Element	Indefinite
*Leptochloa		
Martynia	_Canotia_	Calycoseris
*Olneya	Coleogyne	Chylisma
*Parkinsonia	_Fallugia_	*Dalea
Pectis	_Psilactis_	*Ephedra
*Peucephyllum		PETALONYX
*Palafoxia		Psathyrotes
*Porophyllum		Sphaeralcea
Sesbania		
*_Triodia_		
Tribulus		
Trixis		
*Washingtonia		

It appears by this table that the desert genera fall into three nearly equal groups: namely, those which are found only in one or the other of the two subareas, and those which occur in both

[22] The region bordering the Colorado River is too little known to permit exact statements regarding it. There are reasons for believing that the Colorado subarea should include the interval between the river and the eastern slope of the Providence Mountains.

of them. I have separated the genera of each group into two sections; a northeastern section for those whose extensions are into Nevada, Utah, and the Great Basin life-area; and a south-eastern section to include those whose extensions of range are into Arizona, and towards or into northern Mexico. There remains a group in the third column whose affinities cannot be stated definitely, mostly because represented by more than one species which have diverse ranges. Genera which are represented by species which also extend into the peninsula of Lower California are distinguished by an asterisk. Washingtonia has its only extension in that region.

It is to be noted that Astephanus, the single northeastern genus peculiar to the Colorado subarea, is known from a single collection. All the others are southeastern, and all but ten extend into Lower California. On the other hand Canotia and Fallugia, two of the southeastern plants of the Mojave subarea, are found only in the Providence Mountains, which may belong to the Colorado subarea. Only four of the peculiar Mojavan plants have been reported from Lower California.

Like geographical affinities are exhibited by the different species of certain genera which are differently represented in each subarea. A longer list than the following might be compiled, but these examples must suffice.

DISTRIBUTION OF CERTAIN DESERT SPECIES.

Colorado Subarea	Mojave Subarea
Agave *deserti	Agave utahensis
Aster Orcuttii	Aster tortifolius
Cassia *Covesii	Cassia armata
Coldenia canescens	Coldenia Nuttallii
—— *Palmeri	
Dalea *Emoryi	Dalea Fremonti
—— Parryi	—— polydenia
—— *Schottii	
—— *spinosa	
Gilia *bella	Gilia dichotoma
—— *Schottii	—— Matthewsii
—— *tenuifolia	—— setosissima
Lupinus arizonicus	Lupinus brevicaulis
Pentstemon ambiguus	Pentstemon glaucus
Phacelia micrantha	Phacelia Ivesiana
Psathyrotes *ramosissima	Psathyrotes annua

All the species in the Colorado column have southeastern affinities; all those in the Mojave column have northeastern affinities. In the former, ten out of sixteen extend into Lower California; in the latter, none.

The distribution of the desert flora, and fauna as well, is not known, as yet, with sufficient exactness to permit positive statements. But facts already accumulated indicate that in the Colorado subarea the Lower Sonoran flora, which extends over the entire desert area, is very slightly modified by any other. The Mojave subarea, on the contrary, shows a marked influence from the Great Basin life-area. The limit to which this extends appears to be defined by the Chuckawalla Mountains.

While it is true that, within our territory, the general elevation of the Mojave Desert considerably exceeds that of the Colorado Desert, a difference having an undoubted modifying effect on their floras, yet the precipitation, the temperature, and other conditions of the two subareas are very similar. And the conclusions at which we have arrived would be strengthened were the investigation to be extended so far beyond our limits as to include the depression of Death Valley. Hence it may be inferred that the difference in the character of the two floras is only in part due to climatic causes, but is largely influenced by the topography of the region. In the one case a current of migration was able to pass up, encountering no physical barriers, from Arizona and Lower California into the Colorado Desert; in the other a current from eastern Utah and Nevada would meet no considerable obstacle until it reached the San Bernardino Range and its continuation.

The distinctness of the two subareas is further evident from a consideration of the zonal distribution of their respective floras. Much remains to be learned before these zones can be delimited accurately and finally; but sufficient data are at hand to permit their general disposition to be outlined, leaving the details for completer knowledge.

The Larrea belt, which is considered as indicating the limits of the Lower Sonoran, is present in both deserts. But however useful this shrub may be as the biological index of larger

divisions, it is of less importance in the study of smaller areas. Within these narrower limits it is probable that more than one subzone may be traced, but much fieldwork must be done before this can be accomplished satisfactorily. There are indications, however, in the Colorado Desert of a subzone below the Larrea, whose limits appear to be traceable by the growth of *Atriplex polycarpa*. But for the present the Larrea zone may be taken as a whole, and considered as extending over all parts of the two deserts below 3,000 ^{ft} altitude (915 ^{m}).

Above the Larrea, the zones of the two deserts, although analogous, are indicated by entirely different plants. In the Mojave Desert the first zone above is that of *Yucca brevifolia*. This belongs properly between 3,000 and 4,000 ^{ft} (915–1,220 ^{m}) altitude; occasionally, however, it descends 500 ^{ft} (150 ^{m}) lower, or again carries its characteristic species as high as 7,000 ^{ft} (2,133 ^{m}). In its normal limits *Juniperus californica* is mingled with the Yucca, but does not accompany it far above them. The principal belt of this zone, beginning at the upper end of Antelope Valley, follows the base of the San Bernardino Range to Warrens Wells, and thence, along the Chuckawalla Mountains, at least to Virginia Dale. A less important belt extends from Daggett to Pilot Knob.

Above the first named Yucca belt is the Piñon zone, marked by the presence of *Pinus monophylla*, having an altitudinal breadth between 4,000 and 6,000 ^{ft} (1,220–1,830 ^{m}). It also begins in Antelope Valley, and extends, but with considerable interruptions, from Gormans Station to and beyond Warrens Wells, and possibly even to Virginia Dale.

In the upper end of Antelope Valley the orographical confusion which there exists has given rise to a curious phytogeographical anomaly. Here *Pinus Sabiniana*, *Quercus Douglasii*, and *Q. Wislizeni*, trees characteristic of the western slope of the Sierra Nevada throughout central California, coming through Tejon Pass, find themselves on the *eastern* slope of that range, and the unusual sight is presented of desert foothills clothed with an almost unmixed growth of scrub-oaks. Here, too, are found *Aesculus californica*, *Balsamorhiza deltoidea*, *Gilia tricolor*, *Layia*

heterotricha and *Collinsia Torreyi*, which have entered through the same gate to share the anomalous position of the oaks.

In the Colorado Desert the Yucca zone is replaced by a well-defined zone of *Agave deserti*, which, in an almost continuous belt between the altitudes of 2,500 and 4,000^{ft} (760–1,220^{m}), stretches along the desert slopes of the mountains from San Jacinto Mountain to and beyond the Mexican boundary. The plants of that zone, with inconsiderable exceptions, are quite distinct from those of the corresponding Yucca zone of the Mojave Desert, although it has the same altitudinal limits, and other physiographical conditions.

Above this Agave zone there is a little known Piñon zone. It begins southeast of San Jacinto and extends to El Toro Mountain, above Toros, its upper limit being about 5,000^{ft} (1,525^{m}) above sea level. Possibly, in the little-explored mountains between El Toro and the Mexican line, other traces of this zone may connect it with the extensive nut-pine forests of the peninsula. At its upper end this belt is mainly composed of *Pinos monophylla*, while on El Toro, *P. Parryana* has supplanted it.[23]

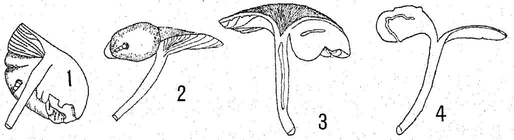
[23] These two species appear either to coalesce, or to hybridize, in this belt. Specimens may be found in which there are, on the same twig, sheaths containing two, three, or four leaves.

[*To be concluded.*]

BRIEFER ARTICLES.

A GALL UPON A MUSHROOM.

WHILE collecting fungi in one of the gorges in the neighborhood of Ithaca, September 12, 1902, I found two specimens of the common *Omphalia campanella* affected by a gall insect. Every fungus collector is familiar enough with the destruction of his choicest mushrooms by insect larvae, but in every case that has been recorded, so far as I can determine, the effect of insect attacks has been exclusively destructive. However completely the fungus may be riddled by larvae, there is ordinarily no growth-response whatever on the part of the plant.



Omphalia campanella Batch.

FIG. 1.—Half of pileus affected by gall insect, showing normal gills and gall viewed from below.

FIG. 2.—Same viewed from the side.

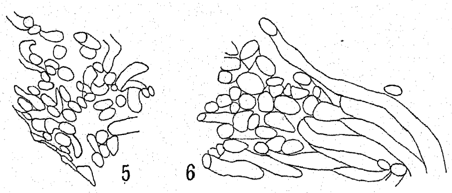
FIG. 3.—Same showing the appearance of the vertical section.

FIG. 4.—Vertical section showing the path of the larva within the gall.

Here we have a very different condition of affairs, as the accompanying figures will show. The normal pileus of *O. campanella* is very thin, in fact less than 1^{mm} in thickness, and with gills attached the entire structure is inside 3^{mm}, as a rule. Here, in contrast, we have a white mass, homogeneous in section, about 8^{mm} in radial diameter, 6^{mm} in thickness, and some 12–15^{mm} in length. Around the ends of the gall, where it adjoins the normal tissue, the even under-surface is broken, as represented in *figs. 1* and *3*, the folds and wrinkles representing gills whose original nature becomes more evident as they approach the normal tissue. The effect upon the upper surface is shown by *fig. 2*. In this the gall causes a marked enlargement, deforming that half of the pileus. The two galls were much alike

in general appearance. There were five larvae in the two together. One of these is sketched in the figures as it was fixed and remained in the opening of its hole. The larvae were determined by Mr. W. A. Riley, of the Department of Entomology of Cornell University, as dipterous larvae of family Mycetophilidae. Further identification was impossible, and since an attempt to cultivate them resulted in the loss of one and the larger part of one gall, the remainder were killed and fixed for study.

To see what changes had occurred in the tissues, portions of one gall were imbedded in paraffin and sectioned for comparison with



Omphalia campanella Batch

FIG. 5.—Camera lucida sketch of normal hyphae.
FIG. 6.—Camera lucida sketch of hyphae from the gall.

sections of a normal Omphalia gathered from the same place. Camera lucida sketches of portions of these sections look at first very much alike. The intercellular spaces are reduced somewhat and the hyphae appear swollen. Measurement of the diameters of a large number of hyphae gives a marked contrast. The average of forty measurements of diameters of cells in the same microscope field was, in the normal tissue, about 7μ; in the gall the average was between 9 and 10μ (*figs. 5*, and *6*). These figures show the stimulating effect of the attack of the gall insect. It has in this case not only produced a relatively very large growth, but has caused a very noticeable increase in the average size of the hyphae (nearly one-third). Hyphae of normal size occur among the swollen threads of the gall, and larger ones are found in the normal tissue, but the averages are strikingly different. A stimulus which is to produce so marked an effect, both in obliterating the lamellae completely and increasing the size of the hyphae themselves, must be applied to the mushroom before gill formation has taken place, else its effect would be destructive, not constructive. It would seem, then, that in these cases the eggs must have been laid very early, so that the abnor-

mal growth kept pace with the larvae, which are comparatively large for so small a mushroom. The hole traced out in *fig. 4* appears to represent the habit of the larva. It has been suggested that most gall insects produce hollow or chambered abnormal growths, and that this may not be a form which habitually produces galls. It is of course possible that the eggs were laid very early and that this stimulus produced a gall, whereas had they been laid later the mushroom would have been destroyed in the ordinary way. The argument that this is a true gall insect would be the size of the gall, and of the larva producing it (5–6^{mm} at least). Larvae as large as these could not work in the ordinary Omphalia pileus because the flesh is too thin and would not offer sufficient food and protection, which is always sought by the insect in laying eggs. It is at least interesting to find such a gall in a group of plants where such a growth has not been reported in our literature. This note, perhaps will bring similar cases to light.—CHARLES THOM, *Cornell University, Ithaca, N. Y.*

SELECTED NOTES. II.—LIVERWORTS.

DUMORTIERA.—Although the genus Dumortiera has as a whole become greatly reduced in the structure of its gametophyte from the typical Marchantia form, and has, generally, hardly a trace left of the complex chambers and nutritive outgrowths characteristic of the group, there are certain species which show, normally or occasionally, enough resemblance to the typical form to leave no doubt that its simplicity is secondary, acquired through retrogressive development from more complex members of the Marchantiaceae. Of the several species of Dumortiera there is only one in which traces of dorsal chambers have been described. This is *D. irrigua* L., which was studied by Leitgeb[1] from herbarium material only. At the growing point on the upper surface he finds and figures quite distinct chambers, without, however, a very definite mouth opening. The upper covering of the chambers becomes broken and disappears more and more on the older part of the thallus, until finally only the basal parts of the chamber walls are left as reticulations on the surface. Leitgeb also mentions "kürzeren oder längeren Haarpapillen" which occasionally arise from the surface of the thallus and represent the cell rows which fill the air-chambers of Marchantia. Campbell (*Mosses and Ferns*) finds no trace of any such complexities on the thallus of *D. trichocephala* from the

[1] Untersuchungen über die Lebermoose, Heft 6, 1881.

Hawaiian Islands.[2] He says: "No indication of lacunae can be seen either near the apex or farther back, the whole thallus being composed of a perfectly continuous tissue without any intercellular spaces." Schiffner[3] describes two species of Dumortiera from Java, *D. trichocephala* and *D. velutina*. Of the first he says: "Frons oberseits ohne oder nur mit zerstreuten Papillen übersät." In neither species does he mention the presence of any trace of air chambers or reticulations. In the possession of numerous papillae on the upper surface *D. velutina* shows itself to be less reduced than *D. trichocephala*.

Z. Kamerling[4] gives a figure of *D. hirsuta* which shows the upper surface thickly covered with unicellular papillae. He refers to Leitgeb's work on *D. irrigua*, but does not mention finding any trace of chambers in *D. hirsuta*. My own observations on the last-mentioned species, which grows rather abundantly in two situations around Chapel Hill, bring out the presence in some cases of air chambers in the young parts of the thallus, which closely resemble those in *D. irrigua*.

Our species, like others of the genus, grows in wet, springy places where the water is constantly trickling through, and it evidently requires more moisture than any other members of the Marchantiaceae (with the exception of Riccia) that occur in this region. Z. Kamerling,[5] in his classification of the Marchantiaceae according to biological types, has considered Dumortiera with good reason as typically hygrophilous, and there seems little doubt that the loss of its air chambers is due to its semi-aquatic life.

The spot where Dumortiera is most abundant here is a gentle rocky slope on the north side of a well-wooded hill, where spring water is constantly oozing out and keeping the thalli saturated. Plants from this place show no air chambers. The other spot where Dumortiera has been found is under a series of overhanging rocks that have been hollowed out so as to form caves 8 to 12^{ft} deep. At the base of these caves the liverwort grows on the damp porous sand, where the water never seems to accumulate so as to cover the plants. Specimens from this situation can be plainly seen with the naked eye to be reticulated over the entire surface, as shown in *fig. 1*, which is from a

[2] See also CAMPBELL, The systematic position of the genus Monoclea. BOT. GAZ. 25: 272–274. 1898.

[3] Die Hepaticae der Flora von Buitenzorg. Leiden. 1900.

[4] Zur Biologie und Physiologie von Marchanticeen. Pp. 73, *pls. 4*. München, 1897.

[5] *Op. cit.* p. 38.

photograph. From sections made through the growing point it could be seen that in the younger parts the air chambers were about as perfect as in Marchantia. Such a chamber is shown in *fig. 2*. It will be noticed that the pore at the top is not so definite as in typical cases, but in every other way the chamber is perfect. There are several cells projecting from the floor, which contain chromatophores and are no doubt the homologues of the filaments filling the chambers of Marchantia, as remarked by Leitgeb. These papillae are not at all abundant, but are scattered here and there, and often persist in the older parts. They were never found to form chains of cells, as in more complex thalli. As they become further and further

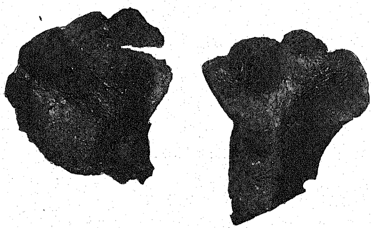


FIG. 1.—*Dumortiera hirsuta.* Two thalli of natural size; from a photograph.

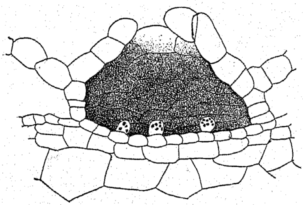


FIG. 2.—The same. Section through an air chamber. ×246.

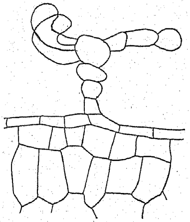


FIG. 3.—The same. Wall of chamber an older part with a few cover cells still attached. × 246.

removed from the growing point, the air chambers become less perfect, the roof cells become torn apart, and many are thrown off, until only a few remain around the upper edge of the wall cells (*fig. 3*). Finally, on the older parts, only the basal cells of the partition are left to form the reticulations seen in *fig. 1*.

It will be seen that we have in *D. hirsuta* chambers and papillae

which almost exactly resemble those found by Leitgeb in *D. irrigua*. They show beyond a doubt that the thallus of Dumortiera has been derived from more complex forms. It seems probable that the comparative darkness of the caves where the plants are found was the factor that induced the formation of the papillae, and that the absence of surface water was favorable to the development of the air chambers.

The "delicate appressed pubescence" mentioned by Underwood (Gray's *Manual of Botany*) as sometimes present on the upper surface of *D. hirsuta* is no doubt the remnants of the air chambers here described.

In his work on the mycorhiza of the Marchantiaceae N. Golenkin[6] could find no trace of fungus in Dumortiera, although he demonstrated it in Preissia, Marchantia sp., Fegatella, and others. I have looked carefully for mycorhiza in Dumortiera, but in no case was any found in the thallus cells. Fungus threads were often seen running up inside the rhizoids, but they were never traced into the living tissue. There is no difficulty in finding abundant mycorhiza in Fegatella.

BLASIA PUSILLA L.—The symbiotic relation of Blasia and Nostoc has often been noted, and Leitgeb (*op. cit.* Heft 1) has given a very good description of the structure and origin of the peculiar chambers of the Blasia thallus in which the Nostoc lives. He failed, however, to get a preparation showing a section of a fully developed chamber with contents, and does not give a drawing that shows the contents. By pressing out the Nostoc he found that the colony was penetrated by clear cells, which he correctly deduces to be branches of the Blasia thallus that have arisen from the slime-secreting hair that was present in the young stages. As the origin of the branched cells ramifying through the Nostoc is so peculiar, I give a drawing (*fig. 4*) that illustrates this point in a mature Nostoc chamber. There grows up from the floor of the chamber a tree-like structure with a single trunk, and from the repeated ramifications of this tree the whole colony becomes interwoven with cells which doubtless serve to abstract nourishment from the algae. This whole ramifying structure has in all probability come, as Leitgeb thought, from the subsequent growth of the slime-secreting cell shown in *fig. 5, s*.

This cell, in the young stage shown, projects upward into the "Blattohr," as Leitgeb calls it, while at the opening at the base on one side the Nostoc enters. This opening is soon closed, and as the cavity

[6] Die Mycorhizaähnlichen Bildungen der Marchantiaceen. Flora 90: 209–220, *pl. 11.* 1902.

grows larger and the Nostoc multiplies, the tree-like upgrowth is produced. In other cases of such symbiotic relationships, as Anthoceros, there are, likewise, cells growing in from the host plant; but in all such cases, so far as I know, these outgrowths originate, not from a common base, but separately and at many points. The striking and beautiful arrangement in Blasia seems to be confined to it alone.

SPHAEROCARPUS TERRESTRIS Smith.—I have found this liverwort abundantly at Chapel Hill, N. C., Selma, N. C., and Florence, S. C. Active spermatozoids were obtained in April of this year from Chapel Hill plants, and it is probable that they are liberated during the greater

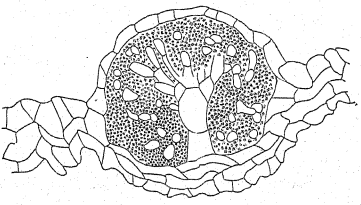


FIG. 4.—*Blasia pusilla*. Section of a large Nostoc chamber. × 166.

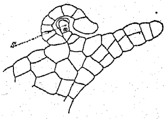


FIG. 5.—Section of a young chamber. × 250.

part of the growing season, as sporophytes of all ages can be found at almost any time.

It is the sterile cells of the sporangium, however, that I wish especially to mention. They are so peculiar in appearance and behavior as to deserve more attention than they seem to have received. These cells, though probably the homologues of the elaters of higher forms, do not bear the least resemblance to them. They are round, have clear cell walls, and contain a good number of bright green chlorophyll granules. These granules retain their bright color almost to the time of the ripening of the spore. They then fade slightly to a yellowish-green, but are still distinctly colored and not the least corroded when the spores are quite ripe. If a ripe black sporangium is crushed under the microscope, these green cells at once attract attention as being totally different from any other sterile cells in the sporangia of either liverworts or ferns. They no doubt carry on photosynthesis to the last moment.

An attempt was made to keep these sterile cells alive on wet filter

paper, in the hope that they might divide; but, although they remain green and intact for more than a week, a gradual fading set in and they finally died. Perhaps they would behave differently in nutrient solution, but I have not yet tried this. Leitgeb (*op. cit.*, Heft 4) also failed in his attempt to sprout these peculiar cells.

In conclusion I wish to express my hearty thanks to Professor Alexander W. Evans for the loan of valuable literature.— W. C. COKER, *University of North Carolina, Chapel Hill.*

CURRENT LITERATURE.

BOOK REVIEWS.

An English class book of botany.

THE EXAMINATION SYSTEM of the higher educational institutions of Great Britain seems to dominate the writing of English text-books. Some such announcement as the following may be found in the preface of most of them: "This work is primarily intended to meet the requirements of students who are preparing for the Intermediate Scientific B.Sc. and Preliminary Scientific M.B. examination of the London University, or for the Advance Stage examination of the Board of Education. But students who intend sitting for other examinations, etc." This shows how heavy a responsibility rests upon the men who set these examinations, and if the subjects and methods they demand be not the ones best suited for training a student in botany—why, so much the worse for the student! The book before us[1] consists of four parts. Part 1 (280 pages) is a description of the structure of plant "types," including the sunflower, bean, elm, mare's-tail, water-lily, maize, yucca, pondweed, pine, selaginella, two ferns, polytrichum, pellia, fucus, ulothrix, spirogyra, vaucheria, haematococcus, agaricus, pythium, mucor, eurotium, yeast, bacteria, physcia; part 2 (130 pages) is concerned with special morphology and classication of angiosperms, under which are the flower and inflorescence, pollination, fruits and seeds, and about sixty pages giving the characters of the orders of angiosperms; part 3 (cut off with 65 pages) treats of the physiology of plants, while part 4 (16 pages) is a running glossary of descriptive terms. The text is reasonably accurate, though by no means flawless, and the book is certainly a compendium of information upon the topics which it treats. As the types are studied in the reverse order from their evolution, a philosophical presentation is practically impossible. Some tables of homologies are given, but the student must hold the facts by sheer strength of memory. The illustrations, "especially drawn for the work," are for the most part extremely crude and some are quite ludicrous. One can hardly imagine that the delineator of a section of a developing ovule (*fig. 84*, II) and of physcia (*fig. 150*) ever saw these structures. The book is not one that will be of service to American students, though it may be helpful to those who are obliged to sit for British examinations.—C. R. B.

Protoplasmic streaming.

A BRIEF ABSTRACT of his extensive work upon this subject was communicated to the Royal Society in February last by Dr. Ewart. Through the gen-

[1] MUDGE, G. P., and MASLEN, A. J., A class book of botany. 12mo, pp. xvi+512, *figs. 228*. London: Edward Arnold. 1903. 7/6.

erous financial aid accorded by the Royal Society he has been enabled to publish the full treatise at the Clarendon Press.[2] Dr. Ewart's observations upon protoplasmic streaming have extended over eight years. The treatise shows complete familiarity with the somewhat extensive literature bearing directly upon this topic, and the prolonged study has enabled him to review much allied work, both physical and physiological. In these days, when hasty publication is too frequent, the author's mature consideration of his theme and the contemplation of it from many sides may be taken as an example worthy of imitation.

Some conclusions of this book have already been stated in the notice of the preliminary paper.[3] The study of streaming itself has brought Ewart to consider so many other aspects of cell physiology that it is not possible to summarize his conclusions without repeating the three or four pages in which he concisely does this. It must suffice to say that he discusses the influence of various external agents (including an extensive study of chemical, mechanical and etherial stimuli) on streaming; the relation between it and the other functions of the cell; the sources of energy; the influence of viscosity, and the ways in which this is modified by various agents; the analogies between streaming and molecular contraction; the transmission of stimuli and the rate of propagation; the existence of nerve fibrillae as claimed by Němec; the movements of chloroplasts; and finally the theories of streaming.

Typographically the book is issued in the same style as the classical textbooks of Sachs, DeBary, Pfeffer, and others, falling below their high standard only in the figures, which are reproduced from rather crude drawings. It would have been worth while to have a good draftsman put these into proper form. One dislikes to see unsightly illustrations in the midst of fine letter press.—C. R. B.

Biological philosophy.

SEEMINGLY almost all the fundamental problems of modern biology are at least touched upon in a curious work which has recently appeared from the hand of Krašan.[4] The book is of a decidedly philosophical nature and is designed as a sort of introduction to broad and deep scientific thinking. Its field is to some extent similar to that of Pearson's *Grammar of Science*, but the present work deals almost entirely with the facts of botany, and the method of treatment as well as the ideas expressed are quite different from those of the *Grammar*. In Krašan's felicitous illustrations and comparisons of things seemingly dissimilar (*e. g.*, of the animate with the inanimate, etc.), is found

[2] EWART, ALFRED J., On the physics and physiology of protoplasmic streaming in plants. Imp. 8vo. pp. viii + 131. *figs. 17*. Oxford: Clarendon Press. 1903.

[3] See BOT. GAZ. 36: 71. 1903.

[4] KRAŠAN, F., Ansichten und Gespräche über die individuelle und specifische Gestaltung in der Natur. 8vo. pp. vii + 280. Leipzig: Wilhelm Engelmann. 1903. *M.* 6.

much to remind the reader of the Weissnichtwo Professor of Things in General; for students who have difficulty in seeing a number of sides to the same question the book will surely be an inspiration. Among the topics discussed are: the relation between material and form throughout nature; metamorphosis and substitution; the relation of species, variety, and race; phylogeny; paleobotany, etc.

The work has an almost medieval smack; after a few introductory pages it is written entirely in dialogue, which may make it tedious for him who is only after the kernel of the nut. There is no doubt, however, that the reader's interest is held by these curiously learned dialogues of Fritz, Hans, and the other students, albeit the ludicrous will occasionally arise to obscure the scientific.—B. E. LIVINGSTON.

MINOR NOTICES.

TREES, SHRUBS, and VINES[5] is a book designed especially for New Yorkers, and to them it may be useful. Though it professes to describe these plants in all the northeastern United States, this part is distinctly inferior and secondary. The greater part of the book is devoted to lists of "these three growths" and to "rambles" in Central Park, whose glories are fully exploited. To a brief description of native trees, shrubs, and vines 172 pages are devoted, and nearly half as much more to the foreign species grown in Central Park. The descriptions are too brief, lacking in contrasts, and often maddeningly comparative. Species of the same genus are often widely separated. The keys are worthless; *e. g.*, one of the chief distinctions is "widely distributed within territory" and "found only on frontier"—exactly the kind of information that one endeavoring to name an unknown tree is unlikely to possess. If the book sailed under true colors it would be more commendable; but judged according to its title it is far inferior to others of like purpose.—C. R. B.

NOTES FOR STUDENTS.

DUDE,[6] studying both fungi and higher plants, finds that the replacement of oxygen by purified hydrogen can be withstood by spores and seeds for a long time (in seeds fifteen to fifty days), but that their germination is much delayed. The vegetative tissues are injured irreparably after an hour or at most a few hours, the younger being most easily killed; yet meristematic tissues endure the hydrogen for three to five days. In all conditions a higher temperature accelerates the action.—C. R. B.

DR. B. LONGO[7] holds that the pollen tube is the only channel by which the embryo of Cucurbita can receive nutriment, because of the marked cutini-

[5] PARKHURST, H. E., Trees, shrubs, and vines of the northeastern United States. 12mo. pp. viii + 451. Illustrated. New York: Charles Scribner's Sons. 1903. $1.50.

[6] DUDE, MAX, Ueber den Einfluss des Sauerstoffsentzuges auf pflanzliche Organismen. Flora **92**: 205–252. 1903.

[7] LONGO, B., La nutrizione dell' embrione delle Cucurbita operata per mezzo del tubetto pollinico. Annali di Botanica **1**: 71–74. 1903.

zation of the cell walls in the chalazal region and of the nucellar epidermis, which is completed while yet the embryo is spherical. The only pervious point is at the tip of the nucellus, where the pollen tube forms a globular swelling and sends branches through the inner integument which extend into the outer. These branches collect the food from the integuments, which are in communication with the nutritive tissues by the vascular bundles, and through the pollen tube it travels to the embryo.—C. R. B.

VINES finds[8] that Buscalioni and Fermi had anticipated some of his studies upon proteolytic enzymes, having determined in 1898[9] by a different method entirely the rather extensive occurrence of such enzymes. In this second paper Vines summarizes their results and contributes further data. He shows that the antiseptic used may influence greatly the digestion (which explains Mendel and Underhill's results with papain); corrects Buscalioni and Fermi's determination that dahlia roots are proteolytically inactive; and finds an enzyme in *Crambe maritima* which belongs to the erepsin group of proteases.—C. R. B.

IN A SERIES of researches on the physiology and morphology of alcoholic ferments, Hansen[10] shows that in beer cultures Saccharomyces spores may develop into sporangia without vegetative division. They simply enlarge enormously and develop new spores in their interior. The maximum and minimum temperatures for growth as well as for sporulation in a number of species of Saccharomyces are given. Temperature does not seem to affect the formation of spores directly; the latter are formed with full access of oxygen and fail to be formed in its absence. Many special variations in the behavior of the different species are noted. Lack of nutriment checks growth, and under certain other conditions may appear to lead to spore production, but it is not itself a cause for this. Several other fungi are considered. Among other points, it is noted that Mucor produces zygospores under the same general conditions as those under which it produces sporangia, but that zygospores need more oxygen for their formation.—B. E. LIVINGSTON.

SPINDLE FORMATION at the first division of the pollen mother-cell of *Larix europaea* DC. has been described in great detail by Dr. Allen.[11] Late in October the pollen mother-cells are easily distinguished, but division does not occur until the following spring. Five stages in the formation of the spindle are described, viz., the preradial stages, the radial stages, formation

[8] VINES, S. H. Proteolytic enzymes in plants. II. Annals of Botany 17:597–616. 1903.

[9] BUSCALIONI and FERMI, Studio degli enzimi proteolytici e peptonizzanti dei vegetali. Annuario R. Ist. Bot. Roma 7:99. 1898.

[10] HANSEN, E. C., Recherches sur la physiologie et la morphologie des ferments alcoholiques. Compt. Rend. Labor. Carlsberg 5:69–107. *figs. 4.* 1902.

[11] ALLEN, C. E., The early stages of spindle formation in the pollen mother-cells of Larix. Ann. Botany 17:281–312. *pls. 14–15.* 1903.

of the felt, the multipolar spindle, and the completion of the spindle. The conclusion is reached that, from the very early prophases, there is present in the cytoplasm a distinct fibrous system which, in conjunction with another set of fibers of nuclear origin, forms the spindle. The fibers of an early reticulum become arranged into a radial system ; this in large part passes into an extra-nuclear felt, and the fibers of the felt form the extra-nuclear portions of the spindle. The fibers are something more than lines of force or expressions of strains or stresses. They are organs with distinct chemical and physical properties which determine their power to do particular kinds of work. No centrosomes were observed at any stage in mitosis.—CHARLES J. CHAMBERLAIN.

H. O. JUEL[12] has recently studied the development of the megaspore in Casuarina, basing his results upon material of an undetermined species collected in Algeria in January 1901, and material of *C. quadrivalvis* collected at Naples in March of the same year. The principal results are as follows: Each of the numerous embryo sac mother-cells, by two successive divisions, gives rise to four megaspores. The cells of the archesporium are distinguished by their larger nuclei and denser contents. The first nuclear division in the megaspore mother-cell is marked by the usual synapsis stage and by a reduction in the number of chromosomes. The number of chromosomes at this divison was not determined definitely, but was not less than eight nor more than twelve, while the number in sporophytic cells was about twice as large. Bodies of kinoplasmic aspect appear at or beyond the poles of the spindle during the mitoses which give rise to the four megaspores, but these bodies are not regarded as centrospheres. They resemble the dense areas which have been described in various gymnosperms. The later stages were not studied, but the writer remarks that in regard to the development of the embryo sac, the entrance of the pollen tube and the formation of the embryo, he can only confirm the account of Treub.—CHARLES J. CHAMBERLAIN.

THE REINVESTIGATION of the fossil, *Williamsonia gigas* Carr.,[13] was suggested by Wieland's researches upon Cycadoidea, and there seems to be considerable resemblance between the two forms.

According to the present account, the structures in *Williamsonia gigas* which have been described as "male flowers" are really the axes of ovulate strobili from which the layer of ovules has become detached after maturity. The staminate structures were probably comparable to those described by

[12] JUEL, H. O., Ein Beitrag zur Entwickelungsgeschichte der Samenanlage von Casuarina. Flora **92**: 284–293. *pl 8.* 1903.

[13] LIGNIER, O., Le fruit du *Williamsonia gigas* Carr. et les Bennettitales, documents nouveaux et notes critique. Mémoires de la Société Linnéenne de Normandie **21**: 19–56. *figs. 9.* 1903.

Wieland for *Cycadoidea ingens.* The fruit of the Bennettitales should be considered, not as a flower, but as an inflorescence.

A diagram showing the relationships of great groups is submitted. From the Protopteridea, the ancestors of the Filicales, is derived a stock which becomes differentiated into two main lines, the Salisburiales and Cordaitales.

At an early period the Cycadales were derived from the Salisburiales and, later, the Coniferales came from the same stock. From the Cordaitales at an early period came the Bennettitales and, later, the Gnetales and Angiosperms. More must be known of the life history of fossil forms lying between pteridophytes and gymnosperms, and also of fossils in these two groups, before a satisfactory diagram of relationships can be constructed.—CHARLES J. CHAMBERLAIN.

ACCORDING TO THE INVESTIGATIONS of J. Brzezinski,[14] the canker disease of trees, long attributed to *Nectria ditissima*, is never caused by this fungus, which, in the opinion of the author, is merely a saprophyte on dead portions of the bark. Inoculations from pure cultures of Nectria failed to produce the disease. The author regards certain bacteria which he found growing in the wood as the true cause of the injury. Three species are described, viz., *Bacterium mali*, *B. pyri*, and *B. coryli*, growing respectively on apple, pear, and hazel. They differ but slightly in cultural characteristics. Inoculations of *B. mali* and *B. pyri* in the wood of apple and pear, respectively, produced discolored areas which gradually extended for a period of several years, forming darkened lines in the wood. In three instances only were small cankers produced on apple trees. The author regards the canker wound merely as one of the external manifestations of the bacteriosis from which the tree is suffering. The disease may manifest itself also as general bacteriosis causing a sickly appearance of the whole tree and producing chlorosis in pear trees. Further, irregular knots on the limbs, a form of twig blight, and root knots are regarded as manifestations of the disease. The twig blight seems to resemble the disease produced on young apple twigs by *Bacillus amylovorus* Burrill. The root knots referred to are "crown galls."—H. HASSELBRING.

PAUL discusses the functions of the rhizoids of mosses and announces certain conclusions,[15] which the writer has held and taught for a number of years, as a result of his observation of the structure and development of these organs. Paul brings no experimental evidence, but relies on more extensive data of the same kind. He holds that the chief function of rhizoids is anchorage; as accessory functions he recognizes (1) the capillary storage and conduction of water by felted rhizoids, and (2) the absorption of water and

[14] BRZEZINSKI, J., Le chancre des arbres, ses causes et ses symptomes. Bull. Acad. Sci. de Cracovie 1903:95–143. *pls. 2–8.*

[15] PAUL, H., Beiträge zur Biologie der Laubmoosrhizoiden. Bot. Jahrb. System. 32:231–274. 1903.

solutes as by any other part of the body. The support for this view is found in the fact that where anchoring organs are most needed there they are developed, and with evident adaptations in form and length of filament to surface and texture of substratum. In epiphytic and rock species they are best developed; in streaming mosses they form a dense tuft with strongly thickened walls, probably variable according to speed of current; but free floating species have no rhizoids. Paul questions the existence of saprophytic mosses, holding that of such species most grow well also on other sub-strata; that the solution of vegetable membranes by rhizoids is improbable; that penetration is made possible by the pioneer activity of other organisms; and that the nutritive activity of the protonema and leaves is adequate. He finds no evidence that the rhizoids of rock species in any way attack or destroy the rocks by secretions. What disintegration they produce is by holding water. He expressly disclaims denying absorption of water and solutes by rhizoids, but holds that this is only such (or even not so much) as other parts of the body do. No secretions by rhizoids dissolve the substratum. Rhizoids are therefore by no means equivalent physiologically to root hairs. —C. R. B.

NEWS.

DR. G. M. HOLFERTY has been appointed instructor in botany in the high school of St. Louis, Mo.

DR. J. F. GARBER has been appointed professor of biology in the state normal school at River Falls, Wis.

MR. H. H. YORK, assistant in botany at De Pauw University, has been appointed fellow in botany in the Ohio State University for 1903.

PROFESSOR J. H. SCHAFFNER, of the Ohio State University, spent the summer vacation continuing his special studies on the flora of Kansas.

DR. T. C. FRYE, professor of biology *ad interim* in Morningside College, Sioux City, Iowa, has been appointed professor of botany in the University of Washington.

MR. EDMUND P. SHELDON has been appointed superintendent of the Oregon State Forestry exhibit for the Louisiana Purchase Exhibition at St. Louis in 1904.

DR. H. C. COWLES is conducting a party from the University of Chicago, which is engaged in ecological work in Arizona. The party will examine the aspects of both desert and mountain floras.

DR. AUGUSTIN GATTINGER, author of a flora of Tennessee and for many years the most active collector in the state, died in Nashville July 18, at the age of seventy-eight. He was a native of Munich.

PROFESSOR HENRY G. JESUP, for twenty-two years professor of botany in Dartmouth College, died June 15 at the age of seventy-seven. He retired from the active duties of his post four years ago and was made professor emeritus.

AT THE University of Minnesota A. M. Johnson has been appointed scholar in botany. Miss Catherine Hillesheim has been appointed assistant on the Geological and Natural History Survey, *vice* Otto Rosendahl who has entered the University of Berlin.

IN THE University of Missouri E. H. Favor, assistant in botany, has been transferred to the department of horticulture; Howard S. Reed, of the University of Michigan, and Charles Brooks, of the University of Indiana, have been appointed assistants in botany.

THE NEW TROPICAL LABORATORY at Paramaribo, of which an account was given by Professor F. A. F. C. Went in the June number of this journal, will be under the direction of Dr. C. J. J. van Hall, who has been appointed

inspector of agriculture for the Dutch West Indies. Dr. van Hall has been botanist at the Phytopathological Laboratory Willie Commelin Scholten at Amsterdam.

PROFESSOR W. A. KELLERMAN and Assistant O. E. Jennings conducted the botanical work of the Ohio State University Lake Laboratory at Sandusky, Ohio, in July and August. Twenty-five students were enrolled. During the latter part of August and early September Professor Kellerman made extensive collections of fungi, especially the parasitic species, on the Cheat Mountains, Randolph county, West Virginia.

THE ORGANIZATION of the Society for Horticultural Science recently proposed has been decided upon. The proposition met with a wide, enthusiastic, and almost unanimously favorable reception, not only by horticulturists, but also by a considerable number of botanists and other scientists. The need of the society is keenly felt and the time appears ripe for inaugurating the new movement. An attendance of at least thirty of those interested is assured for the first meeting, which is to be held in connection with the annual meeting of the American Pomological Society at Boston. Professor L. H. Bailey will preside. A preliminary meeting for organization and conference will be held in the rooms of the Massachusetts Horticultural Society September 9.

MR. CYRUS G. PRINGLE, who last year accepted the position of keeper of the herbarium of the University of Vermont, started from that institution the first of August upon his nineteenth consecutive annual collecting journey to Mexico. Since his return last February he has installed his herbarium at the university and distributed to other herbaria over 30,000 sheets of plants, including his Mexican collections of 1901 and 1902, and that made last January in Cuba. The Mexican collection of 1902 was an especially rich one. Of the 280 species collected for the first time fully one-fourth were new. He will this year continue his explorations of the southern Andean system of Mexico, taking with him one or two assistants. Dr. J. N. Rose, of the National Museum, plans to join him with another assistant in September.

ON ACCOUNT of an unexpected veto by the governor of the appropriation for the New York State College of Forestry, the trustees of Cornell University, at which the college was located, have announced the suspension of this work. The action of the governor is one that cannot be justified from any point of view. A flourishing college had been organized at which several hundred students were in attendance, forestry work upon the reserve in the Adirondacks had been well begun, contracts had been entered into with important wood manufacturing companies for a supply during a term of years, and the whole country was looking to this college with great interest as a well-managed scientific undertaking. We hope that the friends of the college will make known the influences which have brought about this curious action of the governor. It would appear that the trustees of Cornell Uni-

versity might have minimized in some way the injurious veto. Their action in immediately abandoning the Forestry College seems scarcely justified by their public letter.

THE EXPLORATION operations of the New York Botanical Garden in the West Indies have been prosecuted with greater vigor in 1903 than during any previous season. Dr. N. L. Britton and Mrs. Britton made one expedition to the province of Santa Clara in Cuba, accompanied by Mr. J. Shafer, custodian in botany of the Carnegie Museum, Pittsburg, and a second accompanied by Mr. Percy Wilson, of the Garden; Professor F. S. Earle has visited Cuba, Porto Rico, and Jamaica; Dr. M. A. Howe made an extensive collection of marine algae along the coast of Porto Rico; and Mr. George V. Nash, accompanied by Mr. Harry Baker, made collections along the northern side of Hayti. Dr. D. T. MacDougal spent July in Jamaica investigating the facilities afforded for botanical investigations of all kinds by the laboratories and plantations at Cinchona. Professor L. M. Underwood, of Columbia University, also made extensive collections in Cuba and Jamaica by the aid of funds from the Garden and the Hermann Research Fund of the Scientific Alliance: and Professor F. E. Lloyd, of Teachers College, Columbia University, operated on a similar basis in Dominica. All of these expeditions were so carried out that the results accruing to the Garden consisted of living plants, museum and laboratory material, and herbarium specimens. Other collectors visiting this region also furnished material to the Garden. Mr. Percy Wilson made an extensive visit to Honduras to obtain herbarium and museum material, while Mr. L. R. Abrams, of Stanford University, is making an investigation of the flora of southern California by the aid of the Garden. Mr. R. M. Harper, a student of the Garden, has spent the summer in field work in Georgia.

On September 1 Mr. R. S. Williams, who has been appointed collector for the Garden for the Philippines, started for Manila for the purpose of beginning explorations planned to extend over a series of years.

Miss A. M. Vail, the librarian of the Garden, attended the auction sale of the Jordan botanical library in Paris in May, from which over seven hundred volumes were secured for the library.

Dr. Arthur Hollick carried out some investigations of the Cretaceous flora of Long Island for the U. S. Geological Survey early in the year, and spent the summer on detached duty for the same bureau, making an investigation of the fossil flora of the Yukon district. Professor F. S. Earle made a survey of Porto Rico in March for the U. S. Experiment Station Bureau, and Dr. D. T. MacDougal, as a member of the Advisory Board of the Carnegie Desert Laboratory participated in the surveying tour of Mexico and the southwest during February, which resulted in the location of that institution at Tucson, Ariz.

VOLUME XXXVI NUMBER 4

BOTANICAL GAZETTE

OCTOBER, 1903

AN ECOLOGIC STUDY OF THE FLORA OF MOUNTAINOUS NORTH CAROLINA.

JOHN W. HARSHBERGER.

TOPOGRAPHY.

THE mountain region of North Carolina is not a unit, dominated by a single range or group of mountains, but is a complex containing several features of nearly equal topographic importance. These are (1) the Blue Ridge, (2) the eastern Monadnocks and Piedmont valleys, (3) the Unaka Range, (4) the central mountain groups and intermontane valleys.[1]

The Blue Ridge.—The Blue Ridge may be regarded as forming the extreme eastern range of the Appalachian Mountains, carrying the main divide between the Atlantic and Gulf drainage. It reaches its greatest height in Grandfather Mountain, with an altitude of $5{,}964^{ft}$ ($1{,}817^{m}$). Three other peaks reach above $5{,}000^{ft}$ ($1{,}525^{m}$), and a dozen or more, most of them in North Carolina, are above $4{,}000^{ft}$ ($1{,}220^{m}$). The most striking topographic feature of the Blue Ridge is the great difference in slopes on its opposite sides, for it is steep on the eastern and gradual on the western slopes. The eastward-flowing streams have cut back into the mountain belt, and, having the advantage of a more direct course to the sea, have encroached upon the territory of the westward-flowing streams, and have robbed them of portions of their drainage basins.

The eastern Monadnocks and Piedmont Valleys.—The eastern Monadnocks form several groups of mountains along the extreme

[1] HAYES, C. WILLIS, The Southern Appalachians. National Geographic Magazine 1:319.

eastern border of the mountain belt, which have been more or less completely isolated by the erosion of eastward-flowing streams. The most important are the Brushy, South, and Saluda Mountains.

The Unaka Range.—The Unaka Range may be divided into a northern and a southern division. The northern division unites in the region of Grandfather Mountain with the Blue Ridge. From this point due west sixty miles (96^{km}), an irregular mountain mass extends to Paint Rock on the French Broad River. Compared with the Blue Ridge, the Unaka Range reaches a considerably greater average altitude, and contains most of the higher peaks in the southern Appalachians. Not only are these mountains higher, but their slopes are steeper, and their outlines more angular and rugged. The Unakas are equally steep on both sides, and slopes with a descent from crest to stream of $4,000^{ft}$ ($1,220^{m}$) are not uncommon. Many spurs leave the central chain, and between them are deep V-shaped ravines.

Central mountain groups and valleys.—From a commanding position somewhere on the Unaka Range, there may be seen stretching to the east and south a confused aggregation of peaks, ridges, and domes. The cultivated valleys are generally hidden from view, and, except for an occasional clearing and the grassy "balds" on a few of the higher domes, the whole region appears to be covered with a forest mantle. The interior mountains rise to considerable elevations. A very large number of summits reach altitudes between 4,000 and $5,000^{ft}$ ($1,220$–$1,525^{m}$), and a few culminate above $6,000^{ft}$ ($1,825^{m}$). The Black Mountains contain the highest peaks of the Appalachian Mountains, and from Roan Mountain they appear as a huge elongated range, broken into elevated domes, while the range culminates in Mount Mitchell, $6,711^{ft}$ ($2,045^{m}$), the highest point east of the Mississippi and 425^{ft} (130^{m}) higher than Mount Washington. Between these groups, and forming a sort of platform above which they arise, are many broad valleys, commonest toward the head of the streams. Only the smaller streams are flowing at the level of these valleys. Down-stream toward the northwest the broad valleys are found to be more and more deeply cut, until

these occupy deep narrow gorges. The broad valleys must have been formed at base level, before the commencement of the gorge cutting, and they afford the best possible evidence that the altitude of the region in which they are found has been increased by elevation in comparatively recent times.

HYDROGRAPHY.

The waters falling upon the several parts of this future National Park find their way eastward to the Atlantic, or southward directly to the Gulf of Mexico, or to the Mississippi River and thence to the Gulf. The divide between the Atlantic and Gulf drainage follows the crest of the Blue Ridge. The eastward-flowing streams are pressing this divide gradually westward by the capture of territory from less favorably situated streams west of the divide. Northwest of the divide the streams flow at first in the high broad valleys, then in deepening channels, directly to the higher, more rugged Unakas, which they cut through in narrow gorges, emerging upon the Appalachian Valley, those south of New River draining their waters into the Tennessee River.[2]

PHYSIOGRAPHY AND GEOLOGY.

The history of this region, as far as it concerns this paper, begins with the Cretaceous period. At least two great cycles of erosion are recorded in the southern Appalachians, in which the surface of an old continent was worn down from a considerable altitude nearly to base level. Shortly after the close of the Carboniferous period, the entire southern Appalachian province was finally lifted above sea level, and its subsequent history is recorded in the land forms. Following this uplift was a long period, during which the region was subjected to the physiographic processes constituting gradation. Finally, toward the close of the Cretaceous period, the whole province was reduced to a nearly featureless plain, the Cumberland peneplain, relieved

[2] See Hydrography of the southern Appalachian Mountain region. Water Supply and Irrigation Papers. U. S. Geological Survey, nos. 62 and 63. 8vo, 190 pages. Washington. 1902. These two papers by Henry A. Pressey give systematic measurements of the streams in the southern Appalachian Mountain district, and other data of special interest to the ecologist.

only by a few groups of hills where the highest mountains now stand. After the processes of base leveling were nearly completed, that is, toward the close of the Cretaceous period, the region was again uplifted, but unequally, so that at the same time its surface was warped. The streams had become sluggish, but the effect of the uplift was to stimulate them to renewed activity,[3] so that they began cutting upon the last-formed peneplain, a process in which they are still engaged.

PHYSIOGRAPHIC CHANGES INFLUENCING THE DISTRIBUTION OF PLANTS.

Constant change must have taken place in the flora, through the physiographic shifts in the continent, which have been described as taking place in the region of the southern Appalachians. New species were appearing by the process of mutation. Other species were crowded for room by the change of level and the wearing away of strata to which they had adapted themselves, for "if we suppose that the earlier Mesozoic uplands were the seat of the existing dicotyledons, then by the lowering of the surface by gradual consumption of the interstream areas, these forms must have been brought into conflict with the ancient flora of the lowlands and thereby forced into a contest for supremacy."[4] These changes in the physical condition of whole areas produced coincident changes in the constituent plants of the several ecologic regions. Xerophytes were replaced by mesophytes; mesophytes, by the wearing away of the soil and the formation of cliffs by xerophytes. Hydrophytes replaced mesophytes when an area became too wet for the tenancy of ordinary plants. Mesophytes replaced hydrophytes, as a lake area was robbed of its water by some newly encroaching stream. All of these changes were represented in the mountain region of North Carolina, and the plants involved in the readjustment to altered conditions were Cretaceous or Tertiary plants. With the development of the Cumberland peneplain, the forest covering, if one existed at that time (and we have no reason for

[3] HAYES, The southern Appalachians, *loc. cit.* 330.

[4] WOODWORTH, J. B., The relation between base leveling and organic evolution. The American Geologist 14: 231.

believing that a heavy forest did not exist at that early date), was a mesophytic one with the addition of representative herbaceous plants that have not been preserved.

With the uplift of this plain, followed by its planing down by streams, valleys and gorges were created, and rocky strata were exposed, which supported, as such physiographic formations support today, a xerophytic flora. The character of the rocky outcrop influences the particular kind of vegetation, so that we may have a different flora with the same exposure of light, heat, and moisture, if the rocky formations are different. This does not depend so much upon the chemical composition of two different strata, as shown by Cowles,[5] but it is because one formation is further along in its life-history than is the other, so that the vegetation of the clay hill today may be seen on a sand hill in the future. With the widening out of the valley by erosion, and the slackening of the flow of any stream by the reduction of the elevations to base level, the xerophytes of the hillsides will be replaced by the mesophytes of the peneplain. The laws that control changes in the plant covering of a country are, therefore, plainly physiographic and edaphic, if the meteorologic conditions remain the same. We may have broad flood plains, hills, cañons, lakes, and swamps, depending upon the history of the ever-changing topography. Wherever hills are being eroded, rivers widened, waterfalls eliminated, lakes filled, or coastal plains enlarged, there is found a constant change in the plant societies, or a succession in definite order of plant groups. In any land which has undergone degradation from a mountainous topography to a peneplain, we ought to find a marked change in the organisms at the close of the cycle of denudation. In the first stages of change from original constructional topography, effects will be discernible. Sculptured slopes with ravines, sharp divides, and peaks cradle species and varieties by barriers which oppose ingress and egress.

In the progress toward final base leveling, the repeated diversion of the streams, or the reversals of drainage, are a constant

[5] COWLES, H. C., The influence of underlying rocks on the character of the vegetation. Bulletin American Bureau of Geography **2**:— [pp. 26]. Je and D 1901.

cause of changed conditions which Alfred Russell Wallace emphasizes as of importance in the modification of species.[6] The cycle begins in a mountainous tract with least facility for migration of species, and ends in broad lowlands, which favor the easy migration and wide distribution of plants and animals.[7]

The distribution of plants in the region of the southern Appalachians demonstrates the above-mentioned facts. Kearney[8] has called attention to the presence of a Lower Austral (austro-riparian) element in the flora of the mountains of North Carolina. Over one hundred species, which are most abundant and most widely distributed in the austro-riparian area, are known to occur in the mountains at an elevation of 1,000^{ft} (300^{m}) or more. Below that altitude the flora of the southern Appalachian region is mainly Carolinian, and the presence in its midst of numerous austro-riparian forms would be expected. The occurrence, however, of Lower Austral species at higher elevations in the midst of a chiefly transition flora is the noteworthy fact in the distribution of plants in the southern Appalachians. In studying this flora, one soon reaches the conclusion that it comprises two categories of species, which are markedly different, not only in their systematic relationships, present distribution, and past history, but even to a considerable degree in their ecologic constitution. Two types of plants may be distinguished: those of neotropic origin, which have in all likelihood made their first appearance in the Appalachian region in geologically very modern times, probably after the close of the glacial epoch; and those not of neotropic origin, which probably represent the more or less modified descendants of the flora that in later Eocene or Miocene time extended to high northern latitudes, represented in eastern North America by two closely allied species, one in the coastal plain, and the other in the Appalachian region.

In order to explain the facts in the case, botanists have had

[6] WALLACE, A. R., Darwinism, chap. v.

[7] WOODWORTH, J. D., The relation between base leveling and organic evolution. The American Geologist 14:217. 1894.

[8] KEARNEY, The lower austral element in the flora of the southern Appalachian region. Science N. S. 12:831.

recourse to the movement of glaciers southward during the ice age. It appears to the writer that the alternation of cold and warm periods is not necessary to account for the facts described above. An attempt is made in what follows to outline an alternative hypothesis which appears to be a more satisfactory exposition of the case. The elevation of the southern Appalachian region from the Cumberland base level satisfactorily accounts for the differentiation of the corresponding mountain and coastal species. The species now found on the mountains adapted themselves to the higher elevations, and, being more plastic, were wrought upon by the forces which were and are at work in the gradation of the southern Appalachian region. For no fact in biology is better known than the capacity of some species to endure a wide range of physical conditions, while others are fatally sensitive to comparatively slight differences of environment. The modification of the species above mentioned was influenced by the rapid change in the physiography and topography of the country, and not by the glacial ice-sheet, which during a late geologic epoch covered the whole of North America. The oscillations of level are known to have taken place, and it is conceivable that the progenitors of the austroriparian plants of the mountains and coastal plain, specifically identical, mingled when the country was a level peneplain, becoming differentiated as the elevation of the land became more marked. The distribution of plants which represent the characteristic flora of Eocene and Miocene times is thus accounted for.

We have then, in the physiographic changes which have taken place in this mountain region, an explanation of the peculiarities of the flora of the southern Appalachians, which displays certain anomalies of distribution and isolation of monotypic plants. The presence of *Hudsonia montana* Nutt. on the summit of Table Rock is thus explained.[9] Table Rock is an undenuded remnant of a former peneplain, and it is likely that *Hudsonia montana* Nutt. was once more extended in its distribution, but has been isolated by the erosion of the larger part of the plain on which it formerly grew in abundance. *Dicentra*

[9] Collected there by Dr. John K. Small.

eximia DC. is another illustration, growing in a rather restricted area in the Doe River Gorge, where the river cuts between Iron Mountain and Gap Creek Mountain, North Carolina. *Shortia galacifolia* Torr. & Gray, *Lilium Grayi* S. Wats. on Roan Mountain, *Buckleya distichophylla* Torr. on Paint Rock are examples of this same local distribution and isolation.

PHENOLOGIC DISTRIBUTION OF PLANTS.

Four kinds of plants with reference to their phenologic distribution may be distinguished in the vegetation of the forests of eastern North America; viz.: plants of boreal genera (Arctic, Hudsonian, Canadian species), plants of temperate genera (Alleghanian and Carolinian), plants of warmer temperate climate (austro-riparian), and neotropic genera.

Both boreal and temperate species bloom in the spring before they are shaded by the leafing trees, but for different reasons. The plants of temperate origin vegetate and blossom in the spring before the trees are in leaf, because, as a matter of light relationship, it is the only season in which the functions of these plants can be performed adequately, and this presupposes the influence of a certain number of heat units greater than for boreal species and less than for those of more southern origin. A more detailed statement on this subject will be made subsequently. The boreal plants, however, of the eastern Appalachian forests, blossom and vegetate early in the season, because that is the part of the year at which the development of these species, which require a minimum of heat units, is most adequately performed.[10] The writer has shown this in a detailed manner in a paper published in *Science*.[11] The Scandinavian element of our flora consists of plants which mature their seeds quickly before the summer is well advanced. This marks them

[10] The presence of many boreal plants in the forests and peat bogs of the northern states is accounted for by the encroachment of tree vegetation, after the glacial epoch, upon the areas occupied by the boreal plants, which surrounded by the trees, were destroyed or compelled to grow during the period when the trees are leafless. The movement of trees northward was occasioned by the fact that the land area, left bare by the retreat of the glaciers, was one of low tension, while the country to the south, as we have seen, was one of high tension.

[11] HARSHBERGER, The origin of our vernal flora. Science N. S. 1:92–98. Ja 25. 1895.

as physiologically adapted to the influences of a previous short glacial summer. This rapid growth is insured by the activities of the plant during the previous short season in storing up large amounts of reserve material for the next brief season's growth. Even under favorable conditions of summer heat, every external perceptible vital motion in these boreal plants ceases, and it is only after a dormant period of some months, that growth can commence anew. This periodic alternation of vegetative activity and rest is in general so regulated that for a given species of plant both occur at definite times of the year, leading to the inference that the periodicity only depends upon the alternation of the seasons, and, therefore, chiefly upon that of temperature and moisture. The plants of Scandinavian affinity agree physiologically in having a periodic growth and rest. The following diagrams will illustrate this. Diagram *B*, if compared with diagram *A*, shows that the period of vegetative activity of our spring plants of boreal origin corresponds with an arctic or glacial summer, while the dormant period corresponds with an arctic winter, although our present summer has encroached on the former glacial winter.

A. ASTRONOMICAL YEAR DURING GLACIAL PERIOD.

<table>
<tr><td>VEGETATIVE PERIOD</td><td>FLOWERING AND REPRODUCTIVE PERIOD</td><td rowspan="2">DORMANT PERIOD</td></tr>
<tr><td colspan="2">GROWING PERIOD OF PLANTS</td></tr>
<tr><td colspan="2">ARCTIC SUMMER</td><td>ARCTIC WINTER</td></tr>
</table>

B. ASTRONOMICAL YEAR — 1903.

<table>
<tr><td>VEGETATION</td><td>FLOWERS</td><td colspan="2">DORMANT PERIOD</td></tr>
<tr><td colspan="2">GROWING PERIOD OF BOREAL PLANTS</td><td>DORMANCY OF SUMMER ←</td><td>→ DORMANCY OF WINTER</td></tr>
<tr><td colspan="3">PRESENT SUMMER</td><td>PRESENT WINTER</td></tr>
</table>

The plants of warmer temperate climate (austro-riparian species) require a greater number of heat units than those plants just described, and their distribution at present depends largely upon temperature and soil conditions. In the case of the austro-riparian species found in the southern Appalachian mountains, two factors are probably most effective in permitting these species to maintain themselves in what would seem to be an unfriendly environment, viz., amount of insolation and the nature of the soil.[12]

A favorite situation in the mountains for colonies of lower austral species is on the southern exposure of hills, where the angle of inclination and the position with reference to the sun insure the greatest possible amount of insolation. The soil preferred by the great majority of these species is light, sandy, and poor in organic material; it is consequently readily permeable to water and becomes quickly and strongly heated, being thus similar to the soils which cover a great part of the coastal plain.

Unfortunately no phenologic data are at hand with reference to the plants of warmer temperate character. In lieu of exact data, a reference to Chapman's *Flora*[13] may assist in determining the position of these plants with reference to the period of flowering. Those plants not of neotropic origin, which are probably the more or less modified descendants of that characteristic flora which existed in Eocene and Miocene times, and species of genera that appear to be on the wane, blossom in general, according to Chapman, from May to July, and are not looked upon as spring plants, which blossom from March until May. The neotropic element in the flora of the eastern United States is represented by plants that bloom in general from June until October,[14] and are therefore summer and autumn species. This result of a phenologic tabulation of the austro-riparian plants might have been expected, when the origin and physio-

[12] KEARNEY, *loc. cit.* 841.

[13] CHAPMAN, Flora of the southern United States. 3d ed.

[14] Another group of plants, derived like the Cactaceae and Compositae from the southwest, bloom at about the same period as the plants of neotropic origin. See my paper in Science, *loc. cit.*

logic constitution of these plants is taken into consideration; for, according to the laws of temperature control of plants, species of neotropic and warm temperate origin need a large sum of heat units to carry on adequately their life-processes, and these are not properly carried on unless the specific number of heat units is provided in the environment.

INFLUENCE OF GLACIERS ON THE FLORA OF NORTH CAROLINA.

Upon the retreat of the ice-sheet, that portion of the continent north of the terminal moraine was tenanted again by plants that migrated northward, which as species were adapted to a cold temperate climate. A large number of these species came from the southern Appalachians and adjoining regions, where they had remained undisturbed in their original haunts during the long ice age, and were in a plastic condition for growth in a new environment, through the influence of the pressure of species upon each other in their southern home, and through the physiographic vicissitudes to which these fictile forms were subjected. Many species, therefore, growing in the North Carolina mountains, found congenial conditions in the more extensive land areas in the north.

An inspection of the forest maps to be found in the ninth volume of the Tenth Census Report, *Forest Trees of North America*, will show that there is a center of distribution which comprehends the area of the present states of southern and central Pennsylvania, West Virginia, Kentucky, Tennessee, western North Carolina, southwestern Virginia, northern Georgia, Alabama, Mississippi, where the largest number of species of the most important genera of North American deciduous trees will be found. A study of these maps reveals an important fact, that the spread of the species from this common center has been in a series of more or less concentric waves. Three waves may be distinguished. The first wave consisted of the distinctly glacial flora, which skirted the border of the ice-sheet. The second consisted of the present boreal forms, and the third was a wave of deciduous shrubs and trees, oaks, hickories, and a host of others. The species most successfully provided with means of distribution and most easily adjustable extended furthest

from the original home after the glacial epoch, which circumscribed the area of the original dense forest of the Miocene period. The outer confines of any particular genus is usually occupied, as shown in the maps, by a single species. Nearer the center two species are found; still nearer, if the genus is a large one, three, and still nearer four, etc. The position of the various shades of green on the maps suggests the circles of impulse produced when a stone is thrown into a basin of water. Theoretically these waves spread circumferentially in all directions, unless they meet with obstacles, when they are deflected. Similarly, the maps suggest a series of distributional impulses, by which the various species of oaks, ashes, hickories, and chestnuts were forced out from a parent forest of great density into the area left bare by the retreat of the great ice-sheet. The force which impelled this migration outward from the original forest, a relict of the continental forest of Miocene times, was the tension produced by the species associated together and in a struggle for supremacy, as regards room, light, etc. This struggle for existence must have been intense, as evidenced by the great size, height, and straightness of bole of the deciduous forest trees. Only two alternatives were left the species composing this original forest, namely, extinction or migration. Fortunately for the forest, an area of little or no tension was opened up upon the retreat of the glacial ice. The migration from an area of great tension has been and always will be toward an area of little tension.

MacMillan[15] remarks on this point, with reference to the character of the Minnesota flora, that it has been shown that, while the valley of the Minnesota is geographically central, it is by no means botanically central, but, on the contrary, strongly southern and eastern. Bessey[16] has shown that the trees and shrubs of Nebraska have come up the Missouri bottoms and spread from the southeastern corner of the state west and northwest. Mason states that the trees of Kansas show the same

[15] MACMILLAN, The Metaspermae of the Minnesota Valley 758, 759. 1892.

[16] BESSEY, The forests and forest trees of Nebraska. Ann. Rep. State Bd. of Agric. 1899: 79–102.

origin. Adams[17] has demonstrated this clearly in a study of the faunal distribution of animals and in a cursory way with plants.

The marshaling of these facts exhibits the flora of the southern Appalachians and of the mountains of North Carolina in a new light. That the plants of the northeastern and north central United States (except those left as high northern plants on the nunataks and non-glaciated islands and those of cold temperate habit) are derived from the region of the southern Appalachians, adds considerable zest to the study of the flora of these elevated mountain lands.

PRINCIPLES UNDERLYING THE DISTRIBUTION OF PLANTS IN EASTERN AMERICA.

It is advisable at this point to make a restatement of the principles underlying the distribution of plants in eastern America. These statements are derived from the work done by Gray, Hooker, and others on the distribution of North American plants, with additional facts which seem to the writer necessary to mention because of recent work that has been published with reference to the flora of North America in general.

1. Subsequent to the great Cretaceous uplift in a favorable period of mutation, the north temperate regions of Europe, Asia, and America which extended to high northern latitudes became the habitat of dicotyledons and monocotyledons identical as species in most important points.

This region was occupied by a forest of great density,[18] composed of numerous species of trees, shrubs, and herbaceous plants, and these plants were subsequently definitely allocated during preglacial times to certain geographic areas by the planing down of the country to base level.

3. The movement of the glaciers southward over the north-

[17] ADAMS, CHAS. C., Southeastern United States as a center of geographical distribution of flora and fauna. Biological Bulletin **3**: 115–129. Jl 1902.

[18] GRAY, ASA, Sequoia and its history. Proceedings American Association Advancement of Science **21**: 1. 1872. Scientific papers of ASA GRAY **2**: 142; also *ibid.* **2**: 204. *Cf.* GRAY, Forest geography and archœology. American Journal of Science **16**: 85–94; 183–194.

land exterminated the plants of preglacial times without forcing a migration southward, except the northern herbs and trees left on the moraines, unglaciated islands, glacier margins, and nunataks of the great ice field.[19]

4. During the late Pleistocene, and also during the interglacial period, the Scandinavian element of the boreal and north temperate floras was introduced by the migration of plants from Scandinavia by the high northern roadway through northern Europe and Asia to North America, and, as shown, these plants remained on the retreat of the glaciers in the far north, and on the alpine summits of the more elevated mountains, or were held trapped in the cool shade of the north temperate forest or isolated in cold sphagnum bogs.

5. The plants of this north temperate region south of the terminal moraine during glacial times remained, on the retreat of the glaciers, in undisturbed possession of their original habitats. During the ice age they were still further reduced in numbers and influenced in their distribution by the physiographic forces constantly at work in the shaping of the continent.

6. Upon the retreat of the ice-sheet the glaciated area was supplied with plants from two main sources: (*a*) the plants that had maintained themselves in the north during the ice age, and (*b*) the contingent of plants supplied by the territory to the south and east.

7. Conclusively, therefore, the facts indicate the absence of a southern migration of plants.[20] Rather, they point to the glaciers as the important factor in the isolation of such botanic regions as eastern North America and eastern Asia, which perforce show affinities in their floral make-up that can be explained only by reference to the principles aforementioned.

[19] WRIGHT and UPHAM, Greenland icefields and life in the north Atlantic 197–198. 1896.

RUSSELL, Glaciers of North America 86 and 117. 1897; also in Annual Report U. S. Geological Survey 13: 19–21. 1891–92.

WRIGHT, G. FREDERICK, The ice age in North America 57–62. 1891; also American Geologist 8: 330.

[20] This southern migration seems to the writer well-nigh impossible, because it would mean a movement from an area of lower tension to one of higher tension.

8. Following the glacial period the modification of the plants left in the several widely removed continental areas, eastern North America and eastern Asia, became accentuated, as time elapsed, until the similarities which are marked in the plants of preglacial times became less well defined and the differences evident in the two floras become the feature of recent times.

9. These facts argue for a great antiquity of the flora of the mountains of western North Caroliua. The presence of so many peculiar types of plants, not found elsewhere in America and having their closest relatives in eastern Asia, makes it more certain that groups, now broken up and detached, were once continuous, and that fragmentary groups and isolated forms are but the relics of widespread types, which have been preserved in a few localities where the physical conditions were especially favorable, or where organic competition was less severe.

This important principle is evidenced on every hand as a botanist travels through western North Carolina. The large size of the trees, the close commingling in a dense forest of a great variety of species, the graded-down appearance of the land surface, and the rounded contour of the mountains, all impress the fact upon him that the country through which he travels has been subjected through long ages to the continued action of climatic forces which have carved the land into its present form and influenced the character of the vegetal covering. This impression is greatly heightened, if the following nine criteria for determining the centers of dispersal are applied to the study of the region in question:[21]

1. Location of greatest differentiation of type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms.
4. Location of maximum size of individuals.
5. Location of greatest productiveness and its relative stability.
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations, or modi-

[21] ADAMS, CHAS. C., Southeastern United States as a center of geographical distribution of fauna and flora. Biological Bulletin 3: 122.

fications radiating from the center of origin along the highways of dispersal.

9. Direction indicated by biogeographic affinities.

EDAPHIC FACTORS DETERMINING THE CHARACTER OF THE FLORA OF WESTERN NORTH CAROLINA.

The soils of the higher mountains are rather fine and even-grained loams, gray or red in color, or black from organic ingredients; the loamy and generally stiffer subsoils are red or gray. Over the larger part of the area they are derived from the decomposition, *in situ*, of gneiss or gneissic schists, and are sufficiently deep for tree growth, particularly along the lower slopes. In portions of the region the soil derived from slates, quartzite, and metamorphosed sandstones are shallower, thinner, and not so favorable to tree growth.[22] Soil, according to the definition of Professor Dokouchayev, a Russian investigator, is the superficial horizon of rocks in which the general processes and phenomena of weathering, transportation of particles, etc., combine with the biologic processes due to the influence of plants (lichens and alpine plants), animals, and micro-organisms, such as nitrifying bacteria.[23] A forest soil, such as we find in western North Carolina, is an expression, therefore, not only of the physico-geographic, geographic, and geophysic forces which have been brought to bear in its formation, but also of the geobiologic forces which have been at play. A study of any soil cannot fail to reveal many peculiarities of the vegetation that covers it, but it also throws a flood of light upon the succession of floras which may have flourished at any particular time in a given region. To elucidate: the soils of a given territory are influenced by the life-activities (instance the Leguminosae) and the dead remains of plants and other organisms (peat beds, humic compounds, animal manures, guano, etc.). The soil also influences the

[22] PINCHOT and ASHE, Timber trees and forests of North Carolina. N. C. Geol. Surv. Bull. 6: 220. 1897.

[23] SIBIRTZEV, N., Genetic classification of soils. Zapiski Novo-Alexand. Inst. Selsk. Khoz. Lyesov. Memoirs of the Institute of Agriculture and Forestry at Novo Alexandria, Government of Lublin 9^2: 1–23. 1895. *Ibid.*, 11^3: 1–4. 1898. Experiment Station Record 12: 705.

development and the life-activity of these organisms and their decomposition after death. The character of the plant growth, for example, plays not only a direct, but an intermediate rôle in the formation of soil. The relief of the soil has an important influence in determining the drainage, temperature, etc. And lastly, the successive changes which have taken place in the climate, the encroachments of the forests, the spread of marshes, the drying up of the soil, etc., must in their turn influence the character of soils. A knowledge of the laws and the forms of these influences makes it possible to obtain from the study of soils a basis for the reconstitution of the recent past of the country and for sketching its recent geophysic and geobiologic history. An inspection of the soils of western North Carolina reveals a close relationship between the vegetal covering and the soil. There are a number of humus dwellers with ectotrophic and endotrophic mycorhiza. Such plants as the oaks, beeches, chestnuts, poplars, willows, pines, spruces, and firs are provided with ectotrophic mycorhiza and therefore are to a certain extent dependent on the humus of the soil. Without it a dense forest could not exist, and in any region, such as the mountainous area of North Carolina, the luxuriance of the forest is a correlative of the richness of the soil in humus and its mechanical condition, and *vice versa*.[24] Plants with endotrophic mycorhiza also add their quota to the upbuilding and maintenance of the forest litter, and so do many fungi. In North Carolina, as elsewhere, the rotten windfalls and the fallen leaves return many valuable ingredients to the earth. In the North Carolina mountains, if undisturbed by man, a deep soil rich in organic detritus is found, and this clearly points to the long occupation of the territory by dense forests.

These introductory remarks have been made to show the delicate balance which exists between the vegetation of western North Carolina, on the one hand, and the soil and physiographic features, on the other. Constant change has been manifested in

[24] Another indication of a soil rich in humus is a great variety of saprophytic fungi belonging to several well-recognized groups, such as the Polyporei, Agaricineae, etc.

the transformation that has been made from the monotonous plateau of early Cretaceous times, covered with a rather tame flora, to the richly diversified configuration of the mountains and plains of today, clothed with the most magnificent forests (excepting those of the Pacific slope) to be found anywhere in the western hemisphere. The ecologic disposition of the vegetation with reference to the topography next concerns us.

[*To be concluded.*]

A SKETCH OF THE FLORA OF SOUTHERN CALIFORNIA.

S. B. PARISH.

(*Concluded from p. 222.*)

THE CISMONTANE AREA.

THE genera which are confined to this area are more in number than the distinctive genera of both the other areas combined. Some of them have so wide a range as to deprive them of any but the most general phytogeographical value, and these are omitted from the following table. I have designated by an asterisk those genera which are represented by species that come to us from the south; the others are of northern affinity, and, with the exception of a few belonging to the central valley of California, are plants of the Pacific coast flora.

DISTINCTIVE GENERA OF THE CISMONTANE AREA.

Interior Subregion	Coastal Subarea	Common to Both Subareas	
Fimbristylis	*Acalypha	Adenostoma	Eremocarpus
Githopsis	Achyrachaena	Alchemilla	Godetia
*Imperata	Arbutus	Amorpha	Heterotheca
Juglans	Boykinia	Apiastrum	Heteromeles
Koelia	Calamintha	Athysanus	Loeflingia
Lagophylla	*Cneoridium	Baeria	Mecanopsis
Phragmites	*Cupressus	Cardamine	Oenanthe
*Schoenus	Eryngium	Caucalis	Palmerella
Umbellularia	Grindelia	Chlorogalum	Papaver
	*Harpagonella	*Conyza	Pickeringia
	Micromeria	Corethrogyne	Platystigma
	Myrica	Datisca	Platanus
	*Oxalis	Dendromecon	Scrophularia
	Sphacele	Dentaria	Tropidocarpum
		Dicentra	Valerianella

From a study of the distribution of the avifauna of California[24] Mr. Charles E. Kellar was led to propose a transitional area to embrace a strip of territory from the Coast Mountains, and including them, to the sea; and extending from Monterey

[24] KELLAR, CHAS. E., Geographical distribution of land birds in California. Zoe 1: 296, and map.

into Lower California. This area is characterized by the presence of forms from the Pacific coast, the Californian and the Sonoran areas, as these are laid down by Dr. Merriam.[25] The same conclusion is reached by a consideration of the floral distribution of the region. In its upper portion genera and species which are distinctively of the northern coast flora are both numerous and abundant; passing southward these become fewer and rarer. Many entirely fail to reach our part of this area, while others, like *Myrica Californica* and *Arbutus Menziesii,* are here local varieties. On the other hand, distinctively Sonoran plants, such as the yuccas and the Cactaceae, common in the south, drop out as one passes northward. At no point can a dividing line be drawn; and there is an important element of the flora, in considerable part connecting it with that of the Californian area, which is about equally abundant throughout the whole region.

The table last given, of genera exclusively Cismontane, shows but a weak Sonoran element, and from it one might infer that the flora of this area was overwhelmingly Coastal and Californian. But the table exhibits only half the truth, since the Sonoran element is represented mostly by genera which the Cismontane area shares with the Desert. Indeed, so prevalent is this element that it gives the flora an aspect decidedly Sonoran. The abundance of yuccas and the large development of the Cactaceae have been mentioned already. Some other desert plants that pass into the Cismontane are *Prosopis juliflora*, *Bebbia juncea*, *Philibertia linearis*, *Chilopsis saligna*, *Abronia villosa*, *Encelia farinosa*, *E. Californica*, *Viguiera deltoidea* var., etc. Omitting species that merely enter the respective borders of one area or the other through the different passes, there are over forty species of the Desert fairly frequent throughout the Cismontane, or a considerable part of it; on the other hand, hardly a single distinctively Cismontane species more than enters the confines of the Desert.

A small group of plants, which have entered directly from Lower California, inhabit a narrow strip along the coast. Some barely pass our borders; few penetrate very far within it, and

[25] MERRIAM, J. HART, N. Am. Fauna 3, map 5.

the last one disappears at Santa Barbara. They are enumerated below.

PENINSULAR SPECIES ALONG THE COAST.

Acalypha Californica	Cneoridium Californicum	Mamillaria dioica
Agave Shawii	Dithyrea Californica	Opuntia prolifera
Arctostaphylos diversifolia	Frankenia Palmeri	Opuntia serpentina
Baccharis sarothroides	Isomeris arborea	Simmonsia Californica
Beloperone Californica	Iva Haysiana	Viguiera laciniata
Cereus Emoryi		

The Cismontane area comprises two fairly distinct subareas. These probably owe the differences of their floras to the fact that one is more exposed than the other to the fogs and humid air of the ocean. The line separating them follows those elevations which intercept the direct action of these influences; namely, the seaward flanks of the Cuyamaca and Palomar Mountains, the Temecula Range, and the lower hills which continue it beyond the Santa Ana River.

The district between this line and the Pacific Ocean may be called the Coastal subarea; that between this line and the San Bernardino Range constitutes the Interior subarea. The latter subarea includes the San Fernando, San Bernardino, and San Jacinto Valleys. Where the wide Los Angeles Valley opens out to the sea the two subareas coalesce, and some of the most characteristic Coastal species are carried inland to the base of the San Gabriel Mountains.

The most evident characteristic of the Coastal subarea is the prevalence of oaks. Its rolling hills are covered commonly with open groves of *Quercus Engelmanni* and *Quercus agrifolia;* indeed, the first of these oaks and *Rhus laurina* may be considered the characteristic arboreal plants of this subarea. Its chaparral is much more largely composed of scrub-oak, mostly *Quercus dumosa*, than that of the Interior, where *Adenostoma fasciculatum* is the principal shrub. But the Interior subarea differs from the Coastal mostly in a negative way; the latter possessing fully one hundred species which do not extend into the former. Among these are eight species of Atriplex, five each of Chorizanthe and Phacélia, four each of Gilia and Antirrhinum, and three each of Astragalus, Calochortus, Cotyledon, and Salvia.

The species which are restricted to the Interior subarea are comparatively few and unimportant. Some which contrast with Coastal species may be named.

SPECIES RESTRICTED RESPECTIVELY TO THE INTERIOR OR THE COASTAL SUBAREAS.

Interior Subarea	Coastal Subarea
Adiantum Capillus-Veneris	Adiantum emarginatum
Andropogon macrourus	Andropogon saccharoides
Antirrhinum glandulosum	Antirrhinum Nevinianum
Aplopappus linearifolius	Aplopappus ericoides
Artemisia Parishii	Artemisia Palmeri
Boykinia rotundifolia	Boykinia occidentalis
Calochortus Plummerae	Calochortus Weedii
—— splendens	—— Dunnii
Carex Barbarae	Carex spissa
Chorizanthe Fernandina	Chorizanthe laciniata
—— Parryi	—— fimbriata
Euphorbia ocellata	Euphorbia misera
Gilia Californica	Gilia floribunda
Helianthus Parishii	Helianthus Oliveri
Hemizonia Wrightii	Hemizonia virgata
Lathyrus laetiflorus	Lathyrus splendens
Monardella Pringlei	Monardella hypoleuca
Opuntia Bernardina	Opuntia prolifera
Phacelia Davidsonii, var.	Phacelia Douglasii
Ribes glutinosum	Ribes speciosum
Zauschneria Californica	Z. Californica microphylla

There are also certain plants that are confined to the immediate shores of the ocean, either on the sands of the beach, or in the tidal marshes or meadows that occur in some places. These are exhibited in the subjoined table.

LITTORAL PLANTS.

Arenicolous Species	Halophilous Species
Abronia maritima	Astragalus pycnostachys
—— umbellata	Atriplex hastata
Amblyopappus pusillus	Batis maritima
Aphanisma blitoides	Jaumea carnosa
Atriplex leucophylla	Juncus acutus, var.
—— microcarpa	Lasthenia Coulteri
Calandrinia maritima	Monanthochloe littoralis
Convolvulus Soldanella	Salicornia ambigua
Franseria bipinnatifida	—— herbacea
Mesembryanthemum aequilaterale	—— mucronata
—— crystallinum	Scirpus Tatora
—— nodiflorum	Spartina glabra
Oenothera viridescens	Statice Limonum, var.

THE INSULAR FLORA.

The islands of Santa Catalina and San Clemente, situated some twenty miles off the seacoast, have floras of great interest. They are parts of that general coast-island flora which has received no little attention, not only by reason of certain anomalous elements in its composition, but as well from the problems of origin and affinity to which these give rise.

It has been contended that the coast islands are the emergent peaks of a submerged continent, still retaining the vestiges of its peculiar vegetation. Emergent peaks they certainly are, but a more reasonable theory regards them as belonging, not to another continent, but to a chain of mountains paralleling the present Coast Range, now, save for them, sunk beneath the waters of the ocean, whose waves roll over what was once a broad valley separating the two ranges. Under this theory the peculiar insular plants, such as Lyonothamnus and the species of Lavatera, are to be regarded as the remnants of a flora, antedating the period of subsidence, once common to the whole coast region. Preserved by its isolation on the islands, it has perished on the main-land, or is, perhaps, still feebly represented by a few species, such as *Pinus Torreyana* and *Euphorbia misera*, which retain a precarious foothold along the coast.[26]

[26] The following papers will be found of interest to those desirous of studying the insular floras and their relationship and probable origin:

BRANDEGEE, T. S.—Convolvulus occidentalis. Zoe 1:85. Plants of Santa Catalina Island. Zoe 1: 107. Flora of the Californian islands. Zoe 1: 129. Lavatera—is it an introduced plant? Zoe 1: 188. Flora of the Santa Barbara Islands. Proc. Cal. Acad. II. 1:201.

DAVIDSON, GEORGE.—The submerged valleys of the coast of California, U. S. A., and of Lower California, Mexico. Proc. Cal. Acad. III. Geo. 1: no. 1.

GREENE, E. L.—Notes on the botany of Santa Cruz Island. Bull. Cal. Acad. 2: 377. A botanical excursion to the island of San Miguel. Pittonia 1:74.

LE CONTE, JOSEPH.—The flora of the coast islands of California in relation to recent changes in physical geography. Bull. Cal. Acad. 2: 377.

LYON, W. S.—The flora of our southwestern archipelago. BOT. GAZ. 11: 197, 230.

PARISH, S. B.—The Pacific Lavateras. Zoe 1: 300. Southern extension of the range of *Polypodium Scouleri*. Fern Bull. 9:40.

TRASK, BLANCHE.—Field notes from Santa Catalina Island. Erythea 7: 128.

WATSON, S.—Flora of Guadalupe Island, Lower California. Proc. Am. Acad. 11: 105.

YATES, L. G.—Stray notes on the geology of the Channel Islands. Rept. Cal. State Mineral. 9: 171. Insular floras. *L. c.* 179.

The number of the endemic species of plants occurring on the coast islands was claimed, at one time, to be much larger than is admitted at present. Among them are the remarkable monotypic Lyonothamnus, and Lavatera, with four too closely allied species, no two of them found on the same island, a genus which is unrepresented elsewhere in the western world. All the other endemic insular species belong to genera which have representatives on the adjacent mainland. Probably less than thirty of these species are valid, and of these several are no more than robust developments of plants of the neighboring coast. Twelve of them are found on the islands off the Mexican coast, as well as on the Californian islands, so that hardly more than fifteen remain which are peculiar to the latter group.[27] In the subjoined list species endemic to Santa Catalina and San Clemente are in italic; species too closely connected with continental ones, perhaps mere varieties of them, are designated by an asterisk.

PLANTS OF SANTA CATALINA AND SAN CLEMENTE ISLANDS.

Astragalus Nevinii	Galium Catalinense	Lyonothamnus floribundus
*Ceanothus arboreus	Gilia Nevinii	Malacothrix foliosa
**Cercocarpus Traskae*	*Hemizonia Clementina*	—— insularis
*Crososoma Californica	Lavatera assurgentiflora	*Plantago dura*
*Eriogonum giganteum	*Phacelia Lyoni*	Quercus tomentella
Eriophyllum Nevinii		

These distinctively insular species constitute but an insignificant proportion, although a most interesting element, in the plant population of the islands, which, with these exceptions, is made up of species from the neighboring mainland. The islands are therefore to be considered as a subarea of the Cismontane area, and but slightly differentiated from the Coastal subarea.

PHYTOGEOGRAPHICAL DIVISIONS.

In accordance with the views set forth above, the life-areas of southern California are exhibited in the subjoined table. They are provisional merely, for not only does much remain to be learned of the distribution of our flora, but they are based on an examination of the flora alone, whereas the fauna and avifauna

[27] BRANDEGEE, T. S. Zoe 1: 129.

must also be taken into consideration. It is believed, however, that the divisions here laid down will not be greatly modified when all the facts bearing on the problem come to be known.

LIFE AREAS OF SOUTHERN CALIFORNIA.

Provinces	Regions		Areas	Subareas
Boreal	Arctic		Alpine	
	Boreal	Nevadan	Hudsonian	
			Canadian	
			Transition	Upper
				Lower
Sonoran	Lower Sonoran		Desert	Mojave
				Colorado
	Upper Sonoran		Cismontane	Interior
				Coastal
				Insular

The various life-zones in an ideal section across southern California, from the lowest point in the deserts, across the highest mountain peak, to the coast islands, are represented below:

IDEAL SECTIONAL DISPOSITION OF THE LIFE-ZONES.

Alpine

Hudsonian

Canadian

Upper Transition

Lower Transition

Juniperus Zone	Pseudotsuga Zone
Piñon Zone	Interior Subarea
Yucca Zone	Coastal Subarea
Larrea Zone	Littoral Zone
Atriplex Zone (?)	Insular Subarea

INTERRELATIONS OF THE DIFFERENT LIFE-AREAS.

It is not to be understood that these various phytogeographical subdivisions are strictly limited and sharply defined, as they are represented on biological charts. Here, as always, nature does not pass with abruptness from one formation to another; rather one shades gradually into another. Thus we find few, if any, species where boundaries are strictly conterminous. And in passing across the country a successive and continuous disap-

pearance of species is observed, and the appearance of new ones in their places.

Under the varying influences of soil, moisture, exposure, wind currents,[28] and other subtler, and often unrecognizable, causes, adjoining zones interpenetrate and overlap each other in a most irregular manner. Nevertheless they have a real existence and evident boundaries, manifested by the general character of the vegetation. The most unobservant quickly notices the change from one kind of plant growth to a very different kind, as he passes from the Desert to the Nevadan or the Cismontane areas. The trained eye of the botanist notes in each the limits of several subareas, yet detects in each plants seen also in the others.

The interrelation of the floras of the several areas is manifested by the numerous genera which have representative species in each. Most of them show, by the larger number of species growing in it, the area where the conditions are best suited to their development, and, when the preference is well marked, that area may be considered the one to which they specially belong. Some of the larger of these genera are tabulated below:

INTERRELATIONS OF GENERA.

Genera	Species and Varieties			Genera	Species and Varieties		
	Nevadan	Cismontane	Desert		Nevadan	Cismontane	Desert
Allium	3	3	2	Gilia	11	29	19
Arabis	5	1	2	Hosackia	5	19	4
Astragalus	7	6	17	Juncus	6	5	1
Atriplex	0	10	7	Krynitzkia	1	6	11
Calochortus	1	9	3	Lupinus	9	16	3
Carex	23	10	1	Mimulus	10	11	2
Chaenactis	2	3	6	Phacelia	4	16	12
Chorizanthe	2	11	6	Plagiobothrys	1	6	1
Eriogonum	10	9	20	Pentstemon	5	8	6
Trifolium	2	15	0	Ranunculus	5	3	0

While most plants have a definite and often very restricted range, others are able to adapt themselves to such various environments that their limits are circumscribed by no narrower

[28] The influence of wind currents from the deserts is very potent in disturbing the life-zones in the narrow Nevadan belt; and in a similar manner the moist winds from the ocean modify the boundaries of the Interior and Coastal subareas.

boundaries than those of a biological province. Plants such as these are without phytogeographical value in the study of more limited areas. For an opposite reason plants which are very localized are likewise without value. Only those whose limits are neither too widely extended nor too restricted are serviceable to the phytogeographer in determining the biological subdivisions of a region. For this purpose trees and shrubs are more useful than humbler plants. Not only are they more readily observed, but their greater duration requires a closer adaptation to climatic conditions, while their stature and their depth of root render them less immediately dependent on conditions of pure locality, such as surface moisture or shelter.

PHYSIOGNOMIC CHARACTERISTICS OF THE FLORA.

The most striking feature of the southern Californian flora, taken as a whole, is the prevalence of shrubs. The Nevadan is, indeed, largely a forested region; but its open growth is interspersed with vast tracts of chaparral, and altogether fails to produce an effect comparable to the vaster and denser forests of moister climes. Except in the mountains, trees are seldom numerous, and when present form park-like groves rather than true forests. Each region has, too, its meadows, never of large extent, and except in the mountains mostly confined to soils somewhat alkaline.

But throughout the whole territory, shrubs form the common plant-covering of plain and hillside. In the higher mountains impenetrable thickets of *Castanea sempervirens* and *Ceanothus cordulatus* extend for miles. Lower on the Cismontane slope other species of Ceanothus, intermixed with Arctostaphylos, Rhamnus, Ribes, and many other shrubs, cover expanses as wide. To these succeed dense chaparrals of Adenostoma and scrub-oak.

But it is in the deserts that this characteristic is especially developed. Large areas are thickset with opuntias, or with a great variety of other shrubs, daleas, lyciums, ephedras, tetradymias, and many others, whose rigid and thorny growth renders passage painful or impossible. Indeed, in this region, and to a considerable extent in the Cismontane as well, for half the year

the ligneous plants appear to constitute almost the sole vegetation, since the annuals and the aerial parts of most herbaceous plants disappear in the dry season. And even in the rainy months, the superiority of the herbs over the shrubs, in number of species and of individuals, is concealed by their smaller and often insignificant size.

The subjoined table exhibits the vegetative character of the indigenous plants of the different areas. In compiling it I have omitted varieties, doubtful and obscure species, or the few which cannot be satisfactorily credited to any one area. This, it is believed, more fairly represents the prevalent characters of the plant populations, than would the inclusion of every rare and questionable plant.

VEGETATIVE CHARACTERS OF THE FLORA.

Areas	Annuals and Biennials	Herbaceous Perennials	Shrubs	Trees	Total
Desert	167	86	142	9	*404*
Nevadan	79	296	43	19	*437*
Cismontane	359	306	123	25	*813*
TOTAL	*605*	*688*	*308*	*53*	*1,654*

I have classed as trees all those which in southern California commonly attain to fifteen feet (4.5^{m}) in height, and have a tree-like trunk. Of trees $50–100^{ft}$ ($15–30^{m}$) high the Cismontane has six, the Nevadan four, and the Desert one; the Nevadan has six which exceed this height, but the other areas none.

RELATIVE PROPORTIONS OF THE DIFFERENT CLASSES OF PLANTS.

Areas	Annuals and Biennials	Herbaceous Perennials	Shrubs	Trees	Total
Desert	0.41	0.21	0.25	0.03	0.24
Nevadan	0.18	0.68	0.10	0.04	0.27
Cismontane	0.44	0.37	0.15	0.03	0.49
Southern California	0.365	0.415	0.186	0.032	

The figures in the first four columns of the above table show the percentages which the number of species in each class of

plants bears to the whole number of species in each area; those in the footing show the proportion of each class in reference to the whole flora of southern California. The right-hand column shows the proportion which the total flora of each area bears to the whole flora.

It appears by these tables that there is a notable difference in the development of the various classes of plants in the several areas. Thus the Desert has the largest proportion of shrubs and the smallest of perennials herbs—a condition which is exactly reversed in the Nevadan area. The Desert and the Cismontane areas have nearly an equal percentage of annual species, and each has more than twice as many as the Nevadan. It also appears that the Cismontane has nearly as many species as both the other areas combined. The percentage of arboreal species is unexpectedly found to be nearly the same in each region, but could the comparison be made between the number of individual trees in each area, the Nevadan would far exceed the others.

The principal cause of these differences is doubtless to be found in the climatic character of the several areas. The short season of winter rainfall in the two Sonoran areas permits the development of annual plants, but is unfavorable to perennial herbs. The cooler climate, and the numerous living streams and springs in the Nevadan area are more favorable to perennials than are the conditions in the other areas. Why the proportion of shrubby species should be so much smaller in the Nevadan than in either of the other areas is less evident, but it is probably due to the occupation of the land by trees, whose shade discourages the multiplication of shrubs. But it is also a fact that the chaparral of this area, while extensive, is composed of fewer species than is the same formation in the other areas.

ADAPTATION OF PLANTS TO CLIMATIC CONDITIONS.

The chief condition of their environment, as I have already stated, to which the plants of southern California have to adapt themselves, those which are paludose or aquatic excepted, is the aridity of the climate, resulting from prevalent high temperature, and a scanty and irregular precipitation. This necessity to some

extent affects even those plants which inhabit the higher mountains, but in a less degree than those which grow at lower altitudes. The mountain plants have a far greater need of protecting themselves against the low temperature of winter. Hence many of them are perennial herbs, which are able to preserve through the winter the vitality of their roots, safely buried in the soil, although the aerial portions perish from the cold. And as the air is here cooler and moister, more plants are found with broad and unprotected leaves than in the other areas.

It is in these other areas that there is the greatest development of the protective adaptations which enable a plant most fully to utilize a scanty supply of water. The methods by which this is effected are three: by habits of growth; by provisions for storing supplies of water and food in times of plenty as reserves for times of need; and by contrivances for diminishing the loss of water through evaporation.

The first of these methods is well exemplified by most of the xerophytic annuals. They spring up at once after light rains, and put forth no more than a leaf or two before proceeding to the production of a flower and a fruit. If moisture now fails, reproduction is assured; should it continue to be supplied, branches are sent out and flowers and seed multiplied. Thus a plant when receiving only a little moisture may fulfil the cycle of existence and provide for the continuance of its species, without attaining an inch of stature; but under more favorable conditions it may attain dimensions of two or three feet.

The xerophytic perennial herbs make their growth in the wet season, and, in most cases, the aerial stems perish at the beginning of summer. Thus they reverse the seasons, remaining dormant in summer to survive the heat, just as in colder climates they remain dormant in winter in order to survive the cold.

The same reversal of the seasons is the habit of many of the deciduous shrubs. They put forth their new foliage in early winter, make their growth during the wet season, and, ripening their fruits in spring, drop their foliage when the droughts of summer come on, remaining leafless and dormant until its con-

clusion. This may be said to be the rule with desert shrubs, and it also prevails to a considerable degree in the Cismontane area.

The storage of supplies at times when they are attainable, so that vitality may be preserved through a season when they cannot be secured, is provided for by a thickening of either the stems or the leaves.

The engorgement of the underground stem or its buds, whereby bulbs and tubers are produced, is comparatively rare among the plants of our region. Among the xerophilous plants of the Desert there are but two bulbs, *Hesperocallis occidentalis* and *Calochortus Kennedyi;* and there are two species of Psoralea and three or four cucurbits which have tuberous roots. A few plants, like the lomatiums, have thickened roots. In the Cismontane area the list of plants of this kind is longer, but not greatly.

The Cactaceae are our only examples of the modification of the above ground stem for storage purposes. During the wet season these stems become plump and full of sap, but at the conclusion of the dry season, they are shrunken and corrugated. This is especially noticeable in the opuntias, but it may be observed also in the appearance of the ribs or the mamillae of the other genera at the different seasons.

Storage in the leaves is exemplified by the agaves, the cotyledons, and the sedums. The leaves of these plants also become more or less shrunken by the end of the dry season.

But much commoner than these modifications are the protective devices by which transpiration is limited. Few are the plants of the deserts which have not acquired one or more adaptations whereby this result is effected. Some, like canotia, the ephedras, the cereuses, and the echinocactuses, are entirely leafless; others, like the opuntias, *Dalea spinosa,* and *Hoffmanseggia microphylla,* have the leaves few, small, and early deciduous. In plants such as these, the modified epidermis is chlorophyllous and performs the office of leaves. In place of the broad thin leaves displayed by the plants of moist climates, these denizens of the deserts have small and thick leaves, often with revolute edges and pinnate divisions. Very commonly the foliage or the whole plant is protected by a coat of hairs, wool, or scales, a var-

nish, or a powder, from the direct contact of the parching air of their arid habitat.

The same modifications are present also in the plants growing in the other areas, but they are not so marked and so prevalent as in the desert vegetation. The ferns may be taken as an example. Only one desert fern (*Notholaena teñera*) is unprotected by a coating of some kind, and although this has small and rigid leaves, its excessive rarity may be taken as an indication of its ill adaptation to its environment. None of the mountain ferns have protective coatings upon their fronds. Eleven of the twenty species belonging to the Cismontane area are destitute of such protective devices, and nine are furnished with them; the former being the species which grow in cool damp situations, and the latter those affecting habitats where the supply of moisture is less abundant or permanent.

STATISTICS OF CLASSIFICATION.

The following table presents a summary of the distribution of the flora into the several taxonomial categories. The fourth column under the head SPECIES shows the percentage of the species in each class to the total number of species. Only naturalized or adventive plants are included as introduced, no notice being taken of escapes or waifs. These exotics constitute but 7 per cent. of the species of the flora, a proportion smaller than is commonly found.

SYNOPTIC TABLE OF CLASSIFICATION.

TAXONOMIAL CATEGORIES.	FAMILIES		GENERA			SPECIES				VARIETIES
	Native	Introduced	Native	Introduced	Total	Native	Introduced	Total	Per cent.	
Gamopetalae	32	1	216	19	*235*	714	51	*765*	38	55
Choripetalae	63	1	259	27	*286*	813	50	*863*	43	48
Dicotyledones	95	2	475	46	*521*	1,527	101	*1,628*	82	103
Monocotyledones	17	..	85	14	*99*	253	38	*291*	14	22
Angiospermae	112	2	560	60	*620*	1,780	139	*1,919*	97	125
Gymnospermae	2	..	7	..	*7*	21	...	*21*	1	1
Spermatophyta	114	2	567	60	*627*	1,801	139	*1,940*	98	126
Pteridophyta	7	..	20	..	*20*	41	...	*41*	2	2
TOTAL	*121*	2	*587*	*60*	*647*	*1,842*	*139*	*1,981*		*128*

Of the families forty-eight are represented by a single genus each, and thirty-eight of these each by a single species. The families which have the most numerous species are shown below, arranged in the sequence of the species:

GENERA AND SPECIES OF THE LARGER FAMILIES.

Families	Genera		Species		Families	Genera		Species	
	Native	Introduced	Native	Introduced		Native	Introduced	Native	Introduced
Compositae.......	99	13	294	25	Labiatae........	18	3	44	4
Leguminosae....	24	2	149	5	Rosaceae.......	21	..	42	..
Gramineae......	37	13	95	30	Chenopodiaceae.	10	3	36	3
Polygonaceae....	10	..	85	4	Filices.....	13	..	30	..
Scrophulariaceae..	14	1	84	1	Ranunculaceae..	8	..	28	..
Cyperaceae......	8	..	60	..	Cactaceae.......	4	..	28	..
Cruciferae.......	18	5	51	11	Euphorbiaceae..	7	1	24	2
Polemoniaceae...	3	..	55	..	Solanaceae.....	6	..	22	5
Umbelliferae.....	21	6	45	8	Saxifragaceae...	10	..	25	..
Onograceae.....	7	..	53	..	Rhamnaceae....	4	..	21	..
Hydrophyllaceae..	9	..	52	..	TOTAL......	*351*	*47*	*1,323*	*98*

From the above table, it appears that these twenty-one families, being but 17 per cent. of the total number of families, include 71 per cent. of all the species which belong in the flora, and that the first ten families include 52 per cent. of the species. Over 16 per cent. of the entire number of species are found in the Compositae, 8 per cent. in the Leguminosae, 6 per cent. in the Gramineae, and 4 per cent. each in Polygonaceae and Scrophulariaceae.

Some of these families, as the Compositae, the Gramineae, and the Cruciferae, owe their prominence to a large number of genera of a few species each; but in others this is due to two or three genera, or even a single genus which has many species. Thus the large development of the genus Phacelia gives importance to Hydrophyllaceae, of Gilia to Polemoniaceae, and of Carex to Cyperaceae; while the rank of the Leguminosae results from the numerous species of Hosackia, Trifolium, Lupinus, and Astragalus, and that of the Polygonaceae from the many species of Eriogonum and Chorizanthe. In the following table the genera which have fifteen or more species are arranged in the order of their number:

GENERA WHICH CONTAIN THE MOST SPECIES.

Genera	Species	Genera	Species
Gilia	52	Trifolium	20
Eriogonum	41	Atriplex	19
Astragalus	35	Chorizanthe	19
Phacelia	30	Mimulus	19
Carex	30	Juncus	18
Lupinus	27	Pentstemon	18
Hosackia	22	Opuntia	16
Krynitzkia	20	Galium	15

The above sixteen genera contain 401 species, or 20 per cent. of all the species of the region. Except a single species of Trifolium, they are all indigenous. It is worthy of notice that these most largely developed genera, with a few exceptions, are distinctively western American.

AFFINITIES OF THE FLORA.

On a previous page I have attempted to indicate the more immediate sources from which our flora has been derived, but it may not be without interest to glance briefly at its relation to the wider problems of plant distribution. For this purpose the families may be divided into three groups: first, those of such equal development in the several zones as be accounted cosmopolitan; next, those having their greatest development in the temperate zone; and, lastly, those whose centers of development are in or near the tropics.

Such an arrangement is shown in the table on the opposite page; Phytolaccaceae and Dipsaceae being omitted, since they are represented only by introduced species. The columns of percentage indicate the proportion of the number of families in each regional division to the whole number of families in each taxonomial group.

It appears from this table that the families, leaving out of consideration the cosmopolitan ones, which, being of general distribution, have no present signification, are about equally divided between the tropical and the extra-tropical groups; a result to be expected from the geographical and climatic position of the region.

REGIONAL AFFINITIES OF THE FAMILIES.

Taxonomial Categories	Cosmopolitan		Extratropical		Tropical and Sub-tropical	
	Families	Per cent.	Families	Per cent.	Families	Per cent.
Gamopetalae.......	12	37	8	25	12	27
Choripetalae.......	24	38	21	33	18	29
Dicotyledones......	36	38	29	30	30	31
Monocotyledones...	12	70	2	11	3	17
Angiospermae......	48	43	31	28	33	29
Gymnospermae.....	..	..	1	50	1	50
Spermatophyta.....	48	43	32	28	34	29
Pteridophyta.......	4	57	1	14	2	28
Total........	52	43	33	27	36	30

In the next table are exhibited the relations of the native genera and species to the flora of North America. The number of each which extend beyond the North American continent is shown; and those which are confined to it are separated into four geographical subdivisions; namely, those whose range is restricted respectively to southern California, to California, to the region west of the Rocky Mountains, and those which extend further eastward. While the line has been drawn very strictly between plants which are or are not exclusively North American, and as accurately as possible for those confined to western North America, a somewhat laxer rule has been observed for the two smaller subdivisions. These are merely political, and have little phytogeographical significance, and the limits of many of their plants as yet are not known accurately. For these reasons there are included in the number accredited to California, and to southern California, some plants which, while properly belonging to them, extend a little beyond their boundaries.

This table brings out very clearly the distinctively west American character of the flora. Two-thirds of the genera, it is true, extend their range beyond North America; but of the remaining one-third, only 14 per cent. are found east of the Rocky Mountains, while 86 per cent. of this third are confined to the territory west of them, and of these about half

REGIONAL DISTRIBUTION OF GENERA AND SPECIES.

Taxonomic Categories	Genera						Species					
	Endemic						Endemic					
	North American	Western N. American	Californian	Southern Californian	Total	Extra North American	North American	Western N. American	Californian	Southern Californian	Total	Extra North American
Gamopetalae	13	54	16	6	*89*	127	22	250	164	221	*657*	57
Choripetalae	9	42	11	7	*69*	190	55	259	207	187	*708*	105
Dicotyledones	22	96	27	13	*158*	317	77	509	371	408	*1365*	162
Monocotyledones	3	4	3	3	*13*	72	43	88	40	32	*203*	50
Angiospermae	25	100	30	16	*171*	389	120	597	411	440	*1568*	212
Gymnospermae	..	1	..	..	*1*	6	...	13	5	3	*21*	...
Spermatophyta	25	101	30	16	*172*	395	120	610	416	443	*1589*	212
Pteridophyta	..	...	..	..	...	20	4	9	2	6	*21*	20
TOTAL	*25*	*101*	*30*	*16*	*172*	*415*	*124*	*619*	*418*	*449*	*1610*	*232*
Per cent. of native flora	4	17	5	3	30	70	6	33	23	24	87	12

are restricted to California. It will also be noticed that the geographical specialization rapidly increases in passing from the lower to the higher taxonomial groups. Thus all the genera of Pteridophyta extend beyond the North American continent; of the seven genera of Gymnospermae only one is exclusively North American; of the Monocotyledones 15 per cent. are North American, but of the Choripetalae 26 per cent., and 41 per cent. of the Gamopetalae.

Naturally this local differentiation is much more pronounced in the species than in the genera. Less than one-eighth of the indigenous species extend beyond North America. Among the North American species less than 8 per cent. pass beyond the Rocky Mountains; of the species occurring west of that range nearly 60 per cent. are exclusively Californian; of the Californian species over one-half are confined to the southern counties. In the Pteridophyta the species are about equally divided between North American and those of wider distribution; the development of the Gymnospermae is entirely North American; the Monocotyledones are 80 per cent. North American, the Choripetalae 88 per cent., and the Gamopetalae 92 per cent.

COMPARATIVE RICHNESS OF THE FLORA.

A few figures are given below showing the comparative number of species in the southern California and some other floras. The last column indicates the proportion which the species of each flora bears to that of America north of Mexico.

COMPARATIVE TABLE OF FLORAS.

Region	Authority	Date	Area Sq. Miles	Species	Sq. Miles to each Species	Per cent.
N. Am. excl. Mexico	Heller, Cat. N.A. Pl.	1898	.....	14,534	....	..
N. & NW. U. S. Canada, etc.	Britt. & Br., Ill. Fl.	1898	.....	4,162	....	28
Ohio	Kellerman, 4th Cat.	1899	39,964	2,025	19.7	14
Michigan	Beal & Wheeler, Mich. Fl.	1892	56,451	1,746	32.3	12
Montana	Rydberg, Fl. Mont.	1900	145,776	1,676	89.8	11
Alabama	Mohr, Ala. Pl. Life	1901	50,272	2,525	20.0	17
California	Brew. & Wats., Bot. Cal.	1880	156,511	2,956	52.9	20
Southern California	Parish, MS. Cat.	1900	40,889	1,981	20.6	13
Great Britain	London, Cat. 7th Ed.	1877	89,077	1,665	53.5	..

The superiority in number of species of the flora of Ohio, a state having nearly the same area as southern California, is unexpected, in view of the far greater diversity of physical conditions in the latter region. To some extent this is due to an estimate of specific values somewhat more conservative in the enumeration on which the southern California figures are based than obtained in that for Ohio. But mostly it is owing to the fact that the Ohio flora has been long studied, and by numerous able botanists, while our own has had few students, who have worked under disadvantages, and for a relatively short time. Our flora, consequently, is known imperfectly, while that of Ohio has been worked up thoroughly. Additions to it must come mostly from occasional new introductions, or from the segregation of known species. But with us every year's observations of the few resident botanists add a considerable number of species, either new or not previously reported from our region.[29] Other additions are frequently made by those who restudy the accumulated material in the great herbaria. Much territory remains almost wholly unexplored, some of which is certain to

[29] Since my catalogue was completed in 1900 enough additional plants have been reported to make the total number considerably over two thousand.

yield good returns to future explorers. When fully known, the southern California flora will probably contain not less than 2,500 species.

THE CRYPTOGAMIC FLORA.

In this sketch only the Spermatophyta and Pteridophyta have been considered; but below the ferns and their allies lie a series of plants perhaps more numerous than those above them. The relations of these plants, however, to the problems of the life-areas and geographical derivations of a flora is less definite, or at least less understood, than that of the higher groups. Consequently a consideration of them may be omitted in the investigation of these questions, with confidence that a fuller knowledge is not likely to require a reconsideration of the results arrived at.

The information which has been accumulated concerning the representation of these lower plants in southern California is very incomplete. It is almost wholly the result of the labors of two or three students, extended over a short period of time.

The pioneer resident investigator of these, as of the higher plants of the region, was Mr. Daniel Cleveland. In the lower groups he confined his attention to the marine algae of San Diego, and in 1885 published a list of 147 species. Harkness and Moore in their *Catalogue of Pacific coast fungi* (1880) knew of but seven species from the southern counties. More recently Dr. H. E. Hasse has devoted much study to the lichens, the results of which he has made known in several contributions to botanical journals, and by a *Catalogue of the lichens of southern California*, published in 1898. In this are enumerated 304 species, the largest genera being Lecidea, with 65 species, and Lecanora, with 73.

Beyond this almost all that is known of the lower plants of southern California is due to Professor A. J. McClatchie, who in his *Seedless plants of southern California* (1897) laid a broad foundation for future building. A thousand species are catalogued; the lichens are contributed by Dr. Hasse, but the other orders are treated by Professor McClatchie, and are based mostly on his own collections. The Protophyta number 84

species, the Phycophyta 87, the Carpophyta 748, and the Bryophyta 86.

The Musci and Hepaticae appear to be poorly represented in our flora, as might be expected from the arid environment. Of the former Professor McClatchie was able to enumerate but 63, and of the latter but 23, and few additions have since been made to these numbers. This compares poorly with the 312 Musci and the 90 Hepaticae known in the much smaller area of New Jersey.[30]

The lichen flora is more abundant, but is confined to species adapted to arid conditions. Fungi are less abundant than in regions enjoying a moister climate, and this is particularly true of the fleshy fungi. The algal flora, on the contrary, being for the most part unaffected by atmospheric aridity, and enjoying varied environments, is certainly very rich. Of its lower forms the diatoms are abundant and varied, but the desmids, to speak from my own experience, are discouragingly few.

If one descends still lower to those dubious organisms, the Myxomycetes, they also seem to have a very limited representation. For a number of years I have made the collection of the slime-molds a special object, but with very meager results. Only 18 species, representing 12 genera, have been obtained in a condition which permitted determination, a number less than might have been secured in an hour in more favorable climates. I have never found them in abundance, and seldom at all except after long-continued damp and rainy weather.

San Bernardino, Cal.

[30] Britton, N. L., Catalogue of Plants found in New Jersey. 1889.

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

W. F. GANONG.

(*Continued from p. 186.*)

Soil.—Of great importance as an ecological factor is the composition of the soil, physical and chemical. Contrary to the popular belief, the former is at least as important as the latter.

In its physical composition the marsh soil is remarkably homogeneous. Samples taken from the most diverse situations, from the newest layers brought in by the tides, from old long-cropped marsh, from dredgings deep beneath the bogs, are all so alike as to be indistinguishable except for a variation from red to blue in color, and, probably, a somewhat coarser texture of the soil along the banks of the rivers. It is very important to remember, also, that the soil is very deep, even to eighty feet, though usually much less than this. A combination of so homogeneous with so deep a soil must be rare.

In its general characters the dry marsh soil is light brownish red in color, and extremely fine grained in texture. So fine grained is it that only rarely are the individual grains visible to the naked eye. It has no appearance of humus but rather somewhat suggests clay. When the newly deposited layers are exposed to the sun, they harden enough to require a sharp blow to break them, and crack into polygonal areas, concave upward, from a few inches up to two or three feet in diameter, the cracks often being several inches deep and an inch across. When protected from the direct sun, as on the reclaimed marsh, the caking and cracking is much less marked. When again wetted, however, the hard layers melt away into their former state. It sometimes happens on newly plowed ground that a heavy rain

followed by bright sunshine will cause the surface to cake so hard that germinating seeds cannot break through, and much loss is thus caused to crops.

The mechanical nature of the soil will be much more evident from the following mechanical analysis of five selected samples from typical localities, which has been made for me through the kindness of Professor G. E. Stone, of the Massachusetts Agricultural College.

SAMPLES	Water	Organic Matter	Gravel, 2–1 mm Diam.	Coarse Sand, 1–0.5 mm	Medium Sand, 0.5–0.25 mm	Fine Sand, 0.25–0.1 mm	Very Fine Sand, 0.1–0.05 mm	Silt, 0.05–0.01 mm	Fine Silt, 0.01–0.005 mm	Clay, 0.005–0.001 mm	Total
I. Timothy marsh, unplowed for 40 years....	2.200	6.505	.025	.275	4.125	9.360	22.185	36.165	10.390	8.585	99.815
II. Low marsh, with poor vegetation............	2.600	10.920	.000	.400	.285	1.900	1.300	50.110	17.735	10.530	[24] 95.780
III. Brought in freshly by tide...............	1.800	6.200	1.125	3.100	2.025	4.225	45.275	14.125	12.400	9.660	99.935
IV. Blue mud from 18 inches under surface...	3.160	7.360	.125	.325	2.400	6.210	33.885	20.375	10.865	15.200	99.905
V. From River Habitant, N.S.[23]...............	3.400	3.200	.125	.260	1.485	4.060	46.010	26.800	8.710	5.825	99.875

These figures confirm the impression made by the appearance of the marsh soils, that they are, as a whole, of unusually fine texture. This becomes yet more evident when they are compared with the results of similar analyses made of various soils elsewhere (as for example the many published in the *Bulletins* of the Division of Soils of the United States Department of Agriculture).[25] Soils of this degree of fineness are far from those adapted to truck and root crops, and are close to those best adapted for grass and grain crops. The fineness of the soil, with its consequent increase of surface for chemical solution, has an important influence upon its fertility, in rendering more easily available such valuable minerals as it possesses. The marsh soils differ, however, from most other fine soils in the smallness of the proportion of clay in comparison with the silt and fine silt. A

[23] A specimen sent me by Professor Shutt.

[24] Obviously a considerable error here; cause unknown. Probably the entire analysis of this sample is untrustworthy.

[25] Or the synoptical article, "Soils in their relation to crop production," by MILTON WHITNEY, in the Year Book of the U. S. Department of Agriculture for 1894.

microscopical examination of the soil shows that it consists of irregular, very angular grains of many different colors and sizes. Very marked and characteristic, in every one of the very many samples of the soil examined, is the occurrence of fragments of sponge spicules, some of the more marked forms of which are shown in *fig. 6.* While these spicules do not form any considerable part of any particular sample, certainly not 1 per cent., nevertheless their aggregate quantity in the enormous deposit of marsh mud is very great, supposing, as the samples indicate, they are distributed everywhere through it. I do not imagine, however, that their presence has any significance whatever in the ecology of the vegetation.[26] Numerous diatoms of several forms are also present in the mud.

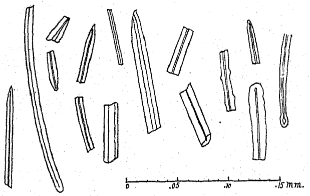


FIG. 6.—Typical forms of sponge spicules from the marsh mud.

The mechanical composition of a soil is important chiefly because of its relation to the supply and circulation of air and water through it. The finer a soil is, other things being equal, the better will it hold water in the hygroscopic state, and hence the better it is for the constancy of water supply to the vegetation. But on the other hand the finer it is the less air will it hold and allow to circulate, and air (*i. e.*, the oxygen) necessary for the respiration of roots is well-nigh as essential a constituent of the soil as water. The soil of the marshes, being much finer than the average, is better than the average for holding and delivering

[26] I think they are without doubt spicules, though they are very fragmentary. They are insoluble in the ordinary acids, and hence are probably siliceous. Very similar forms are figured in the Challenger Report II: *pl. 3, fig. 6,* though I have not seen any branched forms. Two sources of supply are imaginable; living sponges in the Bay and the fossils in the Permo-Carboniferous rocks. But the water must be too muddy for living sponges to flourish, and, moreover, the spicules are very fragmentary, as would be expected if they are ground forcibly out of the rocks, but not if they are floated up from the decay of sponge bodies. Dr. G. F. Matthew tells me fossil sponges are not known from the Permo-Carboniferous rocks.

water, but is worse than the average for aeration. For the latter reason it is adapted only for vegetation with superficial or extremely slender roots, and such the grasses are, while thick-rooted forms, like trees or root crops, needing better aeration, cannot grow, or at least cannot thrive, there.

An extremely important property of soils is their power of circulating water and mineral matters. Every particle of moist soil is surrounded by its film of hygroscopic (and capillary) water holding mineral matters in solution, and these films are in continuity. But the relations of these films to the soil particles and to one another are such that they are, as it were, in a state of unstable equilibrium, so that when water is removed (if not too rapidly) from them at any place, it is restored from neighboring particles, which draw upon others yet more remote, and so on until the equilibrium is restored. And this adjustment is the more perfect the finer the soil. When thus traveling the water carries its dissolved minerals with it. Moreover, owing to the operation of the process of diffusion, the minerals are tending to distribute themselves through the films of water even when these are at rest, from the places where the minerals are more abundant to the places where they are less so. The law of water and mineral movement in soils may be thus expressed: *In a homogeneous soil the water tends to distribute itself evenly throughout the mass, and the soluble minerals tend to distribute themselves evenly throughout the water; a draft at one place upon water and minerals therefore is a draft upon the entire mass if the rate of removal be not more rapid than the equilibrium-restoring power of the soil, which is the higher the finer the soil.* It hence follows that in a homogeneous or nearly homogeneous soil, the plants, if their demands be not greater than the power of the soil to distribute the water, are not dependent for water and minerals simply upon such parts of the soil as can be reached by their roots, but can draw upon the entire mass, the more readily the finer the soil is. Here, I believe, we find the explanation of the lasting quality of the fertility of these marshes when reclaimed; it is due to their depth in combination with their homogeneity, aided by the great water-holding and transferring power given by their fineness of soil. The abundant water

falling upon them as rain, or derived from the melting snows in spring, must saturate the soil to considerable depths, if not to the bottom, thus bringing the water and minerals of upper and lower levels into continuity. Now there is no circulating ground water in the marshes, as the invariable failure of wells dug upon the marshes shows; furthermore they lie below the level of the fresh water of the bogs and mostly below the high-tide level of the sea, and hence there can be no under-marsh drainage, no more indeed than the surface drainage allowed by the shallow ditches or natural runways. This lack of deep drainage has two important consequences; first, there is little or none of that loss of the valuable soluble mineral matters such as is constantly occurring on well-drained upland soils (a fact which alone goes far to explain the lasting fertility), and second, practically the only outlet for the water of the soil is by evaporation from the surface or transpiration through the plants, both of them necessitating an upward movement which tends to bring up the minerals from below. That this effect is actually produced by evaporation is shown by the fact that bald spots even on long-reclaimed, and hence long-drained, marsh always show an efflorescence of salt, and the same is true upon all freshly-exposed surfaces of marsh mud, no matter how long this may have been shut off from the sea. These facts can only be explained by supposing that the salt is brought up constantly from the greater depths. Further, practically the entire vegetation of the marshes consists of the grasses, which both have a comparatively low rate of transpiration themselves, and also protect the ground in an unusual degree from direct evaporation. Hence the upward movement is but slow, and when the warm summer sun promotes transpiration from the plants, the draft made upon the water of the upper soil is not too rapid to allow the latter to recoup itself from the lower layers, and that from a still lower, and so on, to a considerable or even great depth. This upward movement brings with it the minerals, which are not only thus being lifted towards the surface by the ascending water streams, but are constantly diffusing from the lower richer to the upper poorer layers. It can thus come about that the entire depth of the marsh soil is available to the vegeta-

tion above, and it would be only when the minerals from the entire depth are exhausted that the fertility would begin to fail. A corollary of this would be that those marshes whose fertility is most lasting are the deepest, and those soonest exhausted are the shallowest, which certainly agrees in general with the actual facts, as observed and related by those familiar with the marshes.

It is possible that the bogs, which in places underlie the marshes, play some part in this question of water conditions, but we have no facts bearing on this question. As already mentioned, the borings made in the Aulac marsh showed twenty feet of bog lying beneath the eighty feet of marsh mud. Mr. Chalmers is of the opinion that bogs extend practically everywhere beneath the marsh, but I do not think this is probable. If the mode of formation of the marshes in the earlier stages, given earlier in this paper, is correct, it is plain that the marsh could have formed without covering any bog except that which may have existed in the fresh-water lake in this basin before marsh-formation began. Bogs, however, could be buried under mud through natural changes in the courses of the rivers, and they are now often buried in the operations of bog-reclamation. Such places are said to be better drained and to bear larger crops than similar marsh not underlaid by bog.

There are other physical properties of soil of much importance to the vegetation occupying it, such as its permeability to air, its power of absorbing and retaining heat, etc., but for the marsh mud no data at all are available upon these properties.

We pass next to consider the chemical composition of the marsh soil, upon which some satisfactory data are available. Five samples carefully collected by myself in 1898 from different typical situations on the marshes, and of four of which the mechanical analyses have been given on an earlier page (281), have been carefully analyzed for me by the courtesy of Professor Frank T. Shutt, chief chemist at the Chemical Laboratory of the Dominion Experimental Farm at Ottawa, with the following results.[27] To these are added an analysis made at the same lab-

[27] A full discussion of these analyses by Professor Shutt may be found in the Report for 1901, cited in the Bibliography.

oratory, of a similar marsh soil from Cornwallis Valley, Nova Scotia:

Samples	Organic and Volatile Matter	Clay and Sand	Oxid of Iron and Alumina	Lime	Magnesia	Potash	Phosphoric Acid	Soluble Silica
I. Timothy marsh, unplowed for 40 years....	6.54	75.29	14.72	.239	.513	.817	.136	.091
II. Low marsh, with poor vegetation...........	10.60	73.18	12.64	.234	.397	.852	.124	.059
III. Brought in fresh by the tide..............	6.02	75.83	13.79	.652	.283	.902	.146	.063
IV. Blue mud from 18[in] under surface.........	6.77	76.01	14.01	.409	.183	.996	.094	.056
V. From 30[in] below surface under canal above Point de Bute........	3.10	84.48	9.87	.288	.154	.646	.110	0.63
VI. From River Habitant, N. S.................	4.14	75.59	11.71	1.40	.48	.25	.15	......

Samples	Carbonic Acid, &c., Undetermined	Total	Nitrogen	Available.[28] Potash	Available.[28] Phosphoric Acid	Available.[28] Lime	Reaction	Common Salt
I. Timothy marsh, unplowed for 40 years....	1.654	100.0	.182	.0088	.026	.0626	Acid.	.037
II. Low marsh, with poor vegetation...........	1.914	100.0	.338	.034	.016	.0449	Acid.	1.048
III. Brought in fresh by the tide..............	2.314	100.0	.122	.0748	.0466	.397	(*)	4.16
IV. Blue mud from 18[in] under surface.........	1.472	100.0	.106	.0073	.0436	.0792	Acid.	.939
V. From 30[in] below surface under canal above Point de Bute........	1.289	100.0	.062	.030	.0354	.108	Acid.	.217
VI. From River Habitant, N. S.................	......	......	.128	.06	.05	......	......	.86

An abstract of the remarks made upon the samples by the analyst is as follows:

No. I. As to humus (organic matter) nitrogen and lime, about as in soils of average fertility; potash in this as well as the others, much higher than in

[28] The "available" quantities are attained by the Dyer citric acid method. Compare the report by Shutt, just mentioned.

* Neutral or slightly alkaline.

most virgin soils, existing probably as double silicates likely to be gradually liberated in available form by good culture and favorable climatic conditions; phosphoric acid somewhat lower than in virgin soils of average fertility, but a large amount of it is in available form; oxide of iron large in amount, a favorable feature for fertility under proper cultivation; immediately available potash not abundant in this sample, probably because removed for so many years by the hay crop, but available phosphoric acid fairly abundant.

No. II. Shows nearly double the organic matter and nitrogen of no. I; also much richer in potash, total and available, but has less phosphoric acid. If properly drained should give results as good as no. I.

No. III. Of special interest as showing the composition of the original soil as brought in by the tide. Shows nearly three times the lime of nos. I and II, no doubt because so much lime has been removed from the former with the crops.

No. IV. Not positively deficient in substances needful for fertility but mechanically unfavorable. (Compare remarks on these blue soils on the next page.)

No. V. Not appreciably different from the others except in its smaller proportion of nitrogen and humus, which is explained by its deeper position.

No. VI. Not richer in mineral matters than many soils of average productiveness. But a discrimination between the total amounts of the important substances, and the amounts immediately available, shows a remarkably large proportion of the latter, as compared with other fertile soils, and probably in this feature consists a large part of its richness.

With these it is of interest to compare an earlier, and apparently careful, analysis given by Dawson, in his *Acadian Geology* (third edition p. 23) of a "Red soil from Truro, recently deposited":

Moisture		.5	Organic matter	1.5
	Soluble in water		Carbonate of lime	3.60
Chlorine	as common salt	.095	Oxide of iron	2.74
Soda	as common salt	.115	Alumina	1.20
Potash		.013	Magnesia	.11
Sulphuric acid	as gypsum	.073	Soda and potash	.8
Lime	as gypsum	.061	Phosphoric acid	.09
Alumina		.005	Siliceous sand (very fine)	88.00
Magnesia		.004		

Trueman gives some analyses, very imperfect, however, of these soils in his paper (page 104),[29] and some others are found

[29] Eaton, in his most excellent account of the marshes, points out what he thinks a chemical difference between the marshes of Minas Basin and those of Chignecto Bay in that the former contain larger quantities of salts of potash, lime and alumina.

in the various reports of the chemist of the Experimental Farm, cited in the Bibliography.

The marsh soil, however, is not always red and rich, but it is in places blue and barren. This blue soil occurs in low badly drained places, is but a few inches deep, and is underlaid by red soil, which occurs everywhere in a layer under the bogs. Bands of it appear occasionally on river banks in the rich well-drained marsh; but, as already pointed out, this is without doubt due to the wandering of the rivers, which, in changing their courses, cut into spots previously back from their courses and badly drained. The blue soil seems, however, at times to underlie the "sedge-bogs" along the rivers. A full account of the formation of this blue soil is given by Dawson in his *Acadian Geology* (p. 24 of the third edition) as follows:

> The chemical composition of this singular soil, so unlike the red mud from which it is produced, involves some changes which are of interest both in agriculture and geology. The red marsh derives its color from the peroxide of iron. In the gray or blue marsh the iron exists in the form of a sulphuret, as may easily be proved by exposing a piece of it to a red heat, when a strong sulphurous odor is exhaled, and the red color is restored. The change is produced by the action of the animal and vegetable matters present in the mud. These in their decay have a strong affinity for oxygen, by virtue of which they decompose the sulphuric acid present in the sea-water in the forms of sulphate of magnesia and sulphate of lime. The sulphur thus liberated enters into combination with hydrogen obtained from the organic matter or from water, and the product is sulphuretted hydrogen, the gas which gives to the mud its unpleasant smell. This gas dissolved in the water which permeates the mud, enters into combination with the oxide of iron, producing a sulphuret of iron, which with the remains of the organic matter, serves to color the marsh blue or gray. The sulphuret of iron remains unchanged while submerged or water soaked, but when exposed to the atmosphere, the oxygen of the air acts upon it, and it passes into sulphate of iron or green vitriol—a substance poisonous to most cultivated crops, and which when dried or exposed to the action of alkaline substances deposits the hydrated brown oxide of iron. Hence the bad effects of disturbing blue

These substances he supposes to be derived from the trap rocks at the entrance to Minas Basin, which rocks are absent on the Chignecto Branch. Hence he says, the Minas marshes have shown no signs of exhaustion, while the Chignecto marshes have. Comparative analyses of samples from both sets of marshes as far as available do not sustain this contention, nor, indeed, as far as I can learn, is he correct in his estimate of the relative lastingness of the fertility of the two sets of marshes.

marsh, and hence also the rusty color of the water flowing from it. The remedies for this condition of the soil are draining and liming. Draining admits air and removes the saline water; lime decomposes the sulphate of iron and produces sulphate of lime and oxide of iron, both of which are useful substances to the farmer.* [*Since the publication of the first edition of this work, the blue marsh of Nova Scotia has been extensively improved by this process.]

Grouping together the facts as to chemical composition, it is plain that the marsh soil as a whole is rather uniform in composition; that it is chiefly composed of fine siliceous sand with an average of about 10 per cent. of clay; that it naturally contains but little organic matter, which only develops sparingly with the denser vegetation of the reclaimed marsh; that it contains percentages of potash, lime, phosphoric acid, and nitrogen, approximating those of good virgin soils elsewhere, but with an unusually large amount of those substances in an immediately available form; and that the amount of common salt varies with the degree of reclamation. The above facts amply explain the fertility of the marshes, more especially when it is remembered that the chief, almost the sole, crops are grasses, which are not very trying to the soil, and to which the above combination of substances and conditions is particularly favorable. The lasting quality of the marshes is not thus explained, but that, as I have earlier shown, is without much doubt due to their depth and homogeneity, whereby the entire mass to the bottom is made available to the vegetation. These two sets of factors together, I believe, amply explain the agricultural value of the marshes.[30] The composition of the marsh soil as a whole is doubtless very similar to that of the red sandstones of this region (with, perhaps, some salt added from sea-water), which constitute some of the richest upland soils in the provinces. The resemblance is

[30] There is in the marsh country a popular misunderstanding of this subject. It is customary for the residents to say that the analyses of the soil which have been made reveal only clay and sand, with nothing to explain its fertility, which they think must therefore be due to some cause still unknown. No doubt the smallness of the percentages of potash, lime, nitrogen, etc., mislead those unacquainted with the chemistry of soils. In fact the richest soils contain as a rule less than one per cent. of each of those important substances, and quantities much over one per cent., so far from making the soil richer, actually injure it, for the roots of plants are unable to absorb any but very weak solutions of mineral substances.

of course genetic, for the marshes are such soils pulverized and leveled by the sea.

The analyses show further the comparative poverty of the marsh soil in lime, certainly the greatest defect of the marshes, and this substance is the first which has to be added to degenerating marsh. This fact is of much importance ecologically, for to the absence of lime is due the possibility of the formation of sphagnum bogs so extensively developed with the marshes, the sphagnum not growing where lime occurs. The neighboring upland, composed of Carboniferous sandstones, also is free from lime.

The form of occurrence of nitrogen in a soil is very important to its fertility, and as to this the analyses give us no information. The amount of available nitrogen in a soil is closely correlated with the presence of bacteria, and here also, for the marsh soil, we have no data. The bacterial content is not likely to be large, however, since there is so little humus, on which they are dependent.

We must next consider a special phase of soil composition very important to our present subject, namely, the presence in it of common salt (sodium chlorid) derived from the sea water. In minute quantities (small fractions of 1 per cent.) salt in the soil, since it has no part in plant nutrition, does not appreciably affect vegetation as a whole, though it may influence individual forms; but when the percentage rises toward 1 per cent., its presence begins to be of consequence, while above 1 per cent. and upwards it produces profound effects upon the form and distribution of the vegetation. It acts both chemically and physically; chemically in that the plant cannot help absorbing it with the water and it affects injuriously some of the vital processes,[31] and physically because roots are unable to absorb water osmotically (their only method) where more than a very small amount of salt is present. With most roots water cannot be absorbed at all if it contain as much as 1 per cent. of salt and none can absorb it from a solution much, if any, stronger than 3 per cent. As to the amount of salt contained in the marsh soil,

[31] It can of course do this without acting positively as a poison; to what extent the salt is positively poisonous is still uncertain, though the studies of Loeb, True, and others seem to show that in some cases it is so.

that of course varies greatly, as the table on page 286 shows, with the degree of reclamation, etc., and it is this variation which is responsible for the profound differences in the vegetation of the different parts of the marshes. The water of the sea, which has everywhere laid down these marshes, and countless times has overflowed every part of them, must be very nearly the pure salt water of an open sea coast, that is, it must contain near 3 per cent. of salt. This is not only indicated by my tests (unhappily few and crude) of the density of selected samples (tested with an hydrometer), but also by the fact that the fresh-water streams of this region are comparatively insignificant in volume, and the swirling tides mix the fresh water thoroughly with the salt, preventing it from lying on the surface. Not only has every part of the marshes been as salt, or nearly, as the sea, but in places they are much salter, for, owing to the building up of the banks next the sea, there are many pools formed on the marshes into which the highest tides can run, but from which the water does not escape, remaining to evaporate and leave its salt. In many places on the unreclaimed marsh, especially between rivers, such pools exist, much too salt for any vegetation except a few simple algae; and it is quite probable that it is such former pools on the now reclaimed marsh which form the poor or bald places, later to be mentioned, so difficult fully to reclaim. On the other hand, although on the reclaimed marsh no new salt is being added, and the salt already there is being steadily removed by rains, by drainage, and with the crops, it appears never to be entirely removed, no doubt because it is constantly being renewed by diffusion, aided by evaporation, from greater depths. This is shown both by the analyses on page 287 where even the long reclaimed English hay marsh is shown to contain an appreciable amount, and other places a considerable amount, but also by the fact, well known in the marsh country, that an efflorescence of salt ("salt enough to taste," the residents say) is to be seen at times, after dry weather, on the surface of even the oldest reclaimed marsh. Further, the mud brought up from beneath the fresh-water bogs by the canal dredges, shows, as I have myself seen, a marked efflorescence of salt in drying. The

data as to the amount of salt in the reclaimed marsh are unfortunately scanty, but it seems safe to say that it must be on the best marsh much less than half of 1 per cent. and it grades from that upward in all degrees to the wild marsh, which may contain up to 4 per cent., or, in special places, considerably more. It is the presence of this salt even in the reclaimed marsh, which, more than any other cause, keeps the marshes treeless; the salt prevents that ready osmotic absorption essential to large vegetation.

The distribution of salt in the reclaimed marsh is not uniform, however, for places occur in which the vegetation exhibits markedly, or even extremely, a salt-marsh character. These places are of three sorts. First, there occur certain "bald spots," of no apparent determinants, on which only scanty salt-marsh plants grow, or, in certain cases, none at all. These may be remnants of ancient pools mentioned in the preceding paragraph. They can be rendered productive, however, which is effected by covering them with brush (branches of spruce, etc.), straw, loose boards, or other convenient material for two or three years, after which they bear the ordinary grasses of the surrounding marsh. Of course this comes about through the fact that the rain washes out the salt from this soil, and the ground being protected from evaporation, no new supply is brought to the surface by the rising water. Second, on marsh that is improperly drained, there are occasional low spots into which the rain settles from the neighboring higher parts, of course carrying with it some dissolved salt which is concentrated as the water evaporates, thus allowing only a salt vegetation. Third, the farm roads across the marshes, though little used, are always marked by lines of salt plants, often indeed in most striking contrast to the rich hay grasses on each side of them. The presence of the greater quantity of salt along the roads is due, I believe, to a cooperation of two causes; first, the travel over such roads tends to keep down the grasses and to leave the ground somewhat bare, so that evaporation from these places is much more rapid than from the neighboring densely grass-clad ground and the salt must therefore be drawn to the surface more abundantly

there than elsewhere; second, the travel tends somewhat to compact the soil on the roads, and evaporation is more rapid, other things being equal, from a compact than from a loose surface of a homogeneous soil, hence contributing to bring up the salt. In places, too, the roads are lower than the neighboring surface, so that water would tend to drain into them with its salt, which would be concentrated by evaporation; but this is not the main cause of the presence of the salt plants there, for they occur on high as well as low places. On the other hand, the places on the marshes which seem to become most free from salt are three. First, there are the dikes and the ridges thrown up in digging the ditches; the ditch-ridges in particular become so free of salt as to permit not only upland salt-shy weeds to grow but even the still more salt-shy bushes, such as alders, roses, etc. Their freshness is due, no doubt, in large part to the perfection of their drainage, but it is more the result, I believe, of the lack of homogeneous continuity between the somewhat loosely heaped ridge and the compact marsh soil, whereby the continuity of the hygroscopic soil water is interrupted and hence the upward movement by evaporation largely diminished. The comparative looseness and roughness of the ditch-ridges, also, like cultivation in a garden, lessens evaporation, which with the preceding factor permits the removal of salt here to be more rapid than its renewal. Second, there are the spots on good high marsh where hay-ricks have stood, on which a luxuriant weed-vegetation grows up. Plainly the causes are here as above indicated for the bald spots; the ricks preventing evaporation, there is no rise of salt to these places, but rather, by the movement of the water falling here as rain, a washing away of the salt to neighboring places. Much the same effect is produced by the shade of the barns. Third, there are occasional, though rare, spots on the high marsh, not in any way shielded from evaporation, on which weeds, and even small bushes, and in one case a small birch tree, stand. These places appear to me to be always on old and shallow marsh, and represent, I think, spots from which the salt has been in course of time largely removed by drainage and the crops.

Animals.—Animals through divers of their manifold activities may play a large part in phytoecology, but in the case of these marshes their influence appears with but one important exception to be insignificant. That exception is the animal commonly called man, who has developed the habit of providing himself with food by cultivation (in which respect he is by no means unique, but was long anticipated by the fungus-raising ants and others), and to this end has performed two operations of much importance in the ecology of the marshes: first, he has shut out the sea from great areas, thus allowing their conversion from a salt to a nearly saltless soil with the enormous change in their vegetation thus implied; and second, he has brought from other countries certain special kinds of plants which he has let run wild on these marshes. The latter point needs especial emphasis, since it is so liable to be misunderstood. A stranger, even a botanist, visiting for the first time the reclaimed marshes, and looking upon their extensive fields of rich grasses, is likely to think that they are kept in that condition only by careful sowing and frequent renewal, in the absence of which they would soon be replaced by other vegetation. This is what would soon happen on good upland hay fields, for instance, which soon revert to patches of wild weeds and later to forest. But such I believe would be not at all the fate of these marshes. It is of course true that if they were totally neglected by man, the drains would soon fill up, and the dikes would be broken down and washed away, after which the whole region would return to the condition of wild salt marsh. But if, in some way the dikes and drains could be made perpetual, I believe that the present English hay grasses could maintain themselves indefinitely, or at least as long as the fertility of the marshes lasts, without care from man, and they would not as a whole be replaced by any other vegetation. In other words, the English hay grasses brought in by man appear to be the very vegetation best adapted to the conditions prevailing on the reclaimed marsh, and no other, certainly no native plants, could drive them out. Many facts sustain this rather remarkable conclusion, of which the most important is this, universally stated

by those who work with the marshes, that when the marsh is diked and drained, a natural succession of plants follows the freshening of the marsh soil, ending with the English hay grasses, which come in of themselves without any artificial seeding or other aid whatever. They could not do this if there were other plants in the vicinity better adapted to the new conditions. Moreover, having once established themselves in this way, they maintain themselves indefinitely without cultivation. It is true, as already mentioned, that at regular intervals the marsh is generally plowed, but this is by no means to aid these grasses in their competition with other plants, but is mainly to renew the stock on special places to keep it up to the very highest condition of productive vigor. The case of marsh not plowed for over forty years, and still bearing the English grasses with apparently undiminished vigor, shows that the plowing is not essential. Man, therefore, has both created a new field by diking the marshes, and has also brought in a vegetation better fitted than any native vegetation for that field. Later the question of why this introduced vegetation is better than any native kind for this situation will be discussed.

It is an interesting question as to what appearance these great expanses of marsh would present today had man never reclaimed them. We cannot doubt that they would be salt marsh like the still unreclaimed pieces. The fact that the marshes are still sinking, or at least are not rising, would prevent any natural recovery and building up by the action of large vegetation, such as is occurring at the mouth of the Rhone, as described by Flahault and Combres, though were the region rising such a result would probably occur.

As to other animals on the marshes, insects seem fairly abundant, and of course play their part in the pollination of the plants which have showy flowers, but as the greater part of the vegetation is anemophilous, or wind-pollinated, their influence is not ecologically important. Birds occur as in upland meadows. Mosquitoes are abundant and voracious. Various fishes occur in the ditches and canals, and frogs and muskrats are abundant in the fresh-water streams. None of these appears to have any

determinable influence upon the vegetation. An animal important in the economy of soils, namely the common earthworm, is said by the residents not to occur upon the marshes. I have seen what appeared to be their castings, but have been told by an intelligent observing farmer that these are in reality made by some burrowing insect.

Geography of the basin.—To the ecological factors already considered there must be added another of a different sort, namely, the geography of the basin itself. We have already considered one phase of this subject, for upon the latitude, elevation, proximity to the sea, to cold or warm ocean or air currents, depend some of the ecological factors previously discussed. But in addition there are two other important phases of the subject. First, there is the geographical position of the region relative to the great floristic divisions of the earth's surface, upon which depends its flora (as distinct from its vegetation, which is determined by the preceding), and the flora determines the materials upon which the particular ecological factors of the region are to work. In this case we are dealing with a portion of the region covered by the temperate North American flora, with all the peculiarities of species, genera, and families thereto belonging. Second, there is the degree of isolation of the basin from the neighboring regions. Isolation may be brought about principally by the presence of natural barriers, mountain ranges, wide arms of the sea or desert, or even to some extent by great size. Isolation is ecologically important, for upon it depends the possibility of the rapid development of indigenous and exceptionally adapted forms. It produces this result both by preventing the dilution of new adaptive characters through crossing with immigrants from without, and also by preserving undiluted those characters which may be developed independently of adaptation. Regarding now the marsh country from this point of view, we see at once that it is entirely without natural barriers of any kind, and lies open in every direction to immigration from sea-shore, field, and forest; while it is so small in extent (nowhere exceeding four or five miles in diameter), that the natural modes of locomotion of most of the plants

round about can carry them readily to every part of it. Under these circumstances there is not, nor can there be in the marsh-land, any development of extreme adaptations, much less of new types. What happens is this—the ecological conditions here prevailing select from the great mass of forms which are constantly brought to them by natural modes of dissemination, the particular forms that happen to be best adapted to those conditions, rejecting, by suppression, all others. Further, as I believe, having selected the best adapted, their adaptations are in such a basin improved and intensified, so that these forms are being distributed from the basin in a better adapted condition than they enter it. Probably it is a general rule that the larger and more isolated the basin the more the tendency to develop peculiar types; the smaller and less isolated the basin, the more is it a case of selection of forms brought constantly into it and their improvement, such small basins serving as centers of distribution of better adapted forms. The ecological interest of these marshes lies, not in any peculiar adaptations they show, but in the perfection with which they exhibit many phenomena of adaptation.

Summary of the ecological factors; the responsive type of vegetation.

The various physical features we have just considered constitute a set of conditions to which the vegetation must conform. Since no development of a special vegetation to fit them is possible, we ask what forms of the plants of this region do come nearest to fitting those conditions and hence actually occur there. So far as the general climatic conditions are concerned, the responsive type for this region, as I have elsewhere shown,[32] is a mixed mesophytic forest, such as actually occurs on the neighboring uplands. But on the marshes there comes in another factor which is of the first importance and is prepotent or determinative, namely, the peculiar soil. This requires that the marsh vegetation shall be such as has a superficial or very slender root

[32] The vegetation of New Brunswick as a whole I have considered in Bull. Nat. Hist. Soc. New Bruns. 5:52. 1903.

system, thrives in a siliceous and somewhat salt soil, needs a constant rather than a great water supply, can spread a mesophytic foliage to the summer sun and retreat to a winter xerophytic condition, can endure exposure to unshaded sun and strong winds and not spread too great a surface to their transpiring influence, and can use the wind in dissemination and cross-pollination. No one form of vegetation can be found to fit best all these conditions, but any ecologist can tell at once what type comes the nearest to fitting them in the aggregate; it is the grasses and grass-like plants. This is why the vegetation of the marshes is so overwhelmingly of that kind.

The plants of the marshes.

We turn now to consider in some detail the vegetation of the marshland, and naturally ask first what kinds of plants live there. No attempt has yet been made to prepare a flora of the marshes, and such scanty lists of species as exist have already been mentioned (page 162). From the point of view of ecological plant geography, however, their floristic completeness is of slight importance, since the character of the vegetation is determined by only a few prominent forms, and all of those rarer and less conspicuous species, naturally of such interest and importance to the floristic student, might be wanting without affecting the characteristics of the vegetation as a whole. Further, the species, as such, are not of special concern ecologically. What is here important is this, the species as an aggregation of adaptations, that is, as a vegetation- (or life-, or biologic) form, for these vegetation-forms are the unit of the ecologist as the species are of the systematist. In a general way species and vegetation-forms may not be coincident. Thus the same vegetation-form may be developed under similar ecological conditions from very different and widely separate species, as witness Agave-Aloe, Calluna-Erica, and Cereus-Euphorbia (some), but this does not hold true in minutiae, and such forms as those above mentioned, while alike in most characters, differ in many particulars. This is of course because plants are not indefinitely plastic to environmental influences, but are limited much

in adaptation by their heredity, and a different heredity does not permit two distantly related plants to be brought into ecological identity at all points. Hence for purposes of detailed ecological study, and as well because of practical convenience, species and vegetation-forms are coincident, though the point of view from which they are regarded by systematist and ecologist is different. This treatment of the two as coincident is the more necessary at present because of the undifferentiated state of knowledge and terminology of the vegetation-forms,[33] a subject greatly in need of systematic study and formulation. In the following pages I have attempted to indicate a few of the characteristics of the principal species[34] treated as vegetation-forms, especially in the case of *Spartina stricta*, and the ill-success of the attempt is at least in part due to the imperfections in our knowledge of this subject, a matter on which further comment will be found later in this paper. Much work has of course been done upon the anatomy of all of these plants, and Kearney has summarized it in some of the forms, but I have not attempted to treat this phase of the subject.

The vegetation of the marshland.

The vegetation-forms of any region taken together constitute its vegetation. The units, however, are by no means mixed at random to form the mass, but are grouped differentially in

[33] This term, used by Pound and Clements, while better than the "life-forms" of Smith and the "biologic forms" of the translation of Flahault, is far from satisfactory, since the word *form* is somewhat ambiguous and the phrase does not convey an idea of the real significance of the vegetation-form either as a unit of the vegetation, or as a resultant of adaptations. A proper terminology of vegetation-forms (a beginning in which has been made by Pound and Clements) is especially needed in order to allow the forms of different countries to be compared, which they cannot be if simply named for their species.

[34] All of the species listed in the following pages, unless otherwise mentioned, have been confirmed or determined by Mr. Walter Deane, of Càmbridge, Mass., with the exception of a few of the grasses which have been named by Mr. F. Lamson Scribner, of Washington, and to both of these botanists I must express my sincere thanks for their kind aid. The English names given are in all cases those by which the plants are locally known in the marsh country. The nomenclature is that of the sixth edition of Gray's Manual, to which in brackets are added the synonyms made use of in Britton's Manual.

accordance with definite factors. This grouping, and its causes, so far as known, we have now to consider for the marshland.

The vegetation of any region develops, in response to the great primary ecological factors of temperature and precipitation, a characteristic climatic type, which prevails wherever no limiting factor becomes prepotent. For the region in which the marshland lies, this type is a mixed mesophytic forest, as shown upon the neighboring uplands. Further, according to Cowles' theory, which seems to me in general well-grounded, all the vegetation of a region is tending to approach this type, because the vegetation is very closely correlated with physiographic factors, and physiographically any region is in general tending to approach a base-level uniformity. This tendency involves the elimination of prepotent secondary factors, and hence the approach of the vegetation to the climatic type. The marshes appear to offer an exception to this rule, an exception more seeming than real, as will later be noticed.

On the marshland, however, certain limiting factors do become prepotent, determining marked deviations from the climatic type and hence divisions of the vegetation as a whole, namely, *the presence of abundant salt in the soil*, determining a HALOPHYTIC DIVISION, *an accumulation of fresh water* determining a HYDROPHYTIC DIVISION, and *the influence of man*, which removes large sections from the halophytic to the MESOPHYTIC DIVISION, or rather to a special section of it which may be called the *culture section*. The fourth of the principal vegetation divisions, the xerophytic, is not represented in the marshland. These divisions, however, are by no means of homogeneous appearance, but their vegetation falls into distinct groups of plants, the prominent forms of which have the same general aspect and adaptations, and occupy and are correlated with distinct physiographic positions. Such groups are called *formations*. They usually form distinct features of the landscape, and are known by distinctive local names expressing the physical habitat, such as bog, marsh, etc. But the formations, more closely observed, do not show an even mixture of plants, for these are grouped or segregated into definite assemblages, dependent in some part

upon degrees of the physical factors determining the formations, though in larger part upon a quite different principle, namely, the ecological interrelationships of the plants to one another, particularly with reference to the ability of different forms to occupy the same ground at the same time without serious interference and perhaps with positive benefit to one another. Such groups are called appropriately *associations*, and they often are recognized and named locally by the prominent forms, such as oak-forest, broadleaf marsh, etc. Formations and associations are thus both distinct ideas and distinct groups, the former having the physical or physiographic idea prominent, and the latter the idea of ecological interrelationships of the plants, involving their competition and cooperation. Of course the two merge into each other, and often coincide, and by many students they are treated as one. Their delimitation, while often easy, is sometimes very difficult. As in all such cases they can be studied and described only by the selection of typical examples, all intermediate forms being described in terms of the typical. The associations are made up of the *vegetation-forms*, the ecological units, best treated for the present, as above explained, as coincident with species. These vegetation-forms constitute the *members* of the association, but of varying degrees of importance. Some are evidently far in the lead in size, numbers and importance —they are dominant; others are close to these and struggling for the leadership—they are secondary; others are much less conspicuous, but manage to maintain a position among the preceding in spots not occupied by them—they are subordinate. Then in addition to the members may be recognized the frequent visitors from neighboring associations, and various strangers or stragglers from more distant positions. But a satisfactory terminology of the degrees of membership must await an understanding of the real nature of their interrelationship, a knowledge which we do not yet possess.[35]

[35] The distinction here drawn between formations and associations will not be admitted as valid by all, at least to the degree here held, but I believe it represents a real fact in nature and will stand. There is moreover an increasing tendency to recognize the distinction as well as to use this terminology. It is used by Kearney, by Lloyd and Tracy, and by Harshberger (though he calls the association a society).

The various associations of the marshland, named according to their dominant forms, together with their formations to which they belong, are shown by the following synopsis.

Clements lays much stress upon the formation, but gives the association a subordinate place, designating it as "patch." Cowles recognizes formations (under the name of society) but gives no separate importance to the association. Smith recognizes the formation under the name of association, but combines features of both. Warming recognizes the formation (calling it *Verein*), but hardly the association as a distinct group; and the usage is similar in Schimper and Drude. In all these cases, where the one is distinguished and not the other, the facts are of course recognized, though the two groups of ideas are consolidated as it were into one. In such cases the idea of the association is often brought out as a "facies," etc. The complicated history of the use of these terms may be traced in the works of Smith and Flahault cited in the bibliography. The words formation and association as here used seem to me good terms, and should be adopted. The word society could better be restricted to those ecological groups of another kind, such as epiphytes, parasites, etc. Clements has recently made a carefully considered proposal for nomenclature of formations, and I have given some of his names later in this paper. The associations are best distinguished by their dominant forms with the termination *etum*.

[*To be continued.*]

BRIEFER ARTICLES.

A NEW SPECIES OF GEASTER.

(WITH TWO FIGURES)

IN February 1903, I received through Dr. W. C. Coker, of the University of North Carolina, Chapel Hill, N. C., a pretty little Geaster, growing on the bark of moss-covered living trunks of trees in the woods. The first specimens which I received were collected by one of the students at the University, Mr. C. A. Shore, and afterwards very abundant material was collected both by Mr. Shore and Dr. Coker.

The species is quite remarkable in several respects. In the first place, its habitat on bark of living trees is unusual, for while now and then a species normally growing on the ground or on dead logs may be found around the bases of trees on the dead bark among moss, the distinctive habit of this species is upon the dead bark of living trees some distance from the ground. In this respect it is similar to the puff ball, *Lycoperdon leprosum* B. & R.[1] In fact, it sometimes grows intermingled with specimens of *Lycoperdon leprosum* on the same tree, so it may occur as an associate, or as the only puff ball on the tree. Thus far it has always been found among moss, and it will be interesting to know if there is any mutualism between the moss and its associate Geaster, of such a nature that the Geaster is dependent upon the moss, or whether the conditions of moisture, etc., which are favorable for the growth of the Geaster in all cases observed, bring about also the development of the moss, so that the association of the two is merely accidental.

It is also remarkable in another respect, that it belongs to the fornicate section of the genus, a section which contains but a very few species in comparison with the large number known. The third unusual character of the species is that the spores are smooth; not echinulate or tuberculate, as in other species, although the spores are more or less irregular, with three to four slight angles in side view. Usually these angles are not prominent, and under the low power of the microscope the spores appear to be perfectly globose. At first

[1] *Lycoperdon leprosum* B. & R., Rav. Fung. Am. Ex. no. 14. See also Pk. Mon. Lycop. 29.

I thought the spores were white, and they are colorless in specimens which are not very mature, but when the plant is quite mature, the inner peridium well opened and more or less collapsed, the spores mostly have a pale yellowish-brown color. The plant is attached to the moss and the bark by numerous threads, which radiate irregularly from the outer cup-shaped layer of the outer peridium, and the mycelium extends also into the dead bark, penetrating more clearly through the lines of cleavage in the bark, both radial and tangential.

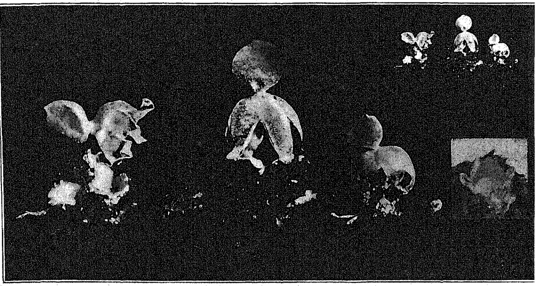


FIG. 1.—*Geaster leptospermus.* Smaller plants, upper right hand corner, natural size. Others $\times$ 2.5, the one at the left collapsed and broken away from cuplike base, which is also collapsed, but is shown as a well formed and distinct layer. Plant at extreme right in early stage of dehiscence; outer peridium split into 4 rays.

In some cases delicate rhizomorphic strands are developed quite abundantly in the tangential cleavage planes. The plants are whitish, but when mature pale gray in color. They are oval to globose, 3–4.5^{mm} in diameter. Before the dehiscence of the outer peridium takes place, the plants are inconspicuous and appear as minute rounded bodies, or minute convex whitish surfaces in the moss. But after dehiscence takes place the fornicate character of the plant lifts the inner peridium so far above the moss that it is quite conspicuous, except for its minute size. When dehiscence of the outer peridium first takes place it splits radially into three or four rays, showing the white granular surface of the inner peridium, with its well defined mouth, which is radiately silky, but not sulcate nor striate. The inner face of the outer peridium is also seen to be granular. As the plant expands more the inner layer of the outer peridium separates from the outer

layer and is everted, the points of the rays remaining attached to the points of the outer cup-shaped layer. The inner peridium is globose and borne aloft as usual. When fully expanded the inner surface of the outer peridium has a white or flesh colored tinge, and under the lens is minutely granular. The inner peridium and area about the mouth is white, while the other portion is whitish or pale lead color. By the time the perforation appears at the center of the mouth the inner peridium is $2.5–3.5^{mm}$ in diameter and is sessile or only very slightly pedicellate.

The cup-shaped outer layer of the outer peridium is quite distinct and well formed, although it is quite firmly attached to the moss and bark and is very thin, the margin of course being split into a number of rays corresponding to the rays of the inner layer.

At my request Mr. J. M. Van Hook, assistant in the botanical department, photographed the plant, one photograph being taken with the plant enlarged two and one-half times to show more of the detail, while another photograph was taken natural size (*fig. 1*). The cup-shaped outer layer of the outer peridium, while intact, does not show very well in the photograph, because, being almost completely immersed in the moss, it could not be sufficiently lighted and brought into focus, though in one of the individuals, which was more or less removed from the moss, the outer layer being torn apart shows more distinctly.

The capillitium is white or pale yellowish, or pale yellowish-brown. It extends from the inner surface of the inner peridium toward the center. The threads are nearly straight, or very flexuous and irregular, the larger and more irregular ones being nearer the peridium. The threads are often flexuous and branched, but are sometimes unbranched for long distances. Their surface is smooth, except that it is often very irregular and more or less corrugated. They vary in diameter from $2–6\,\mu$. The spores are very minute, $1.5–2.5\,\mu$ in diameter, white or very pale yellowish-brown, not echinulate nor tuberculate, many of them showing that they are more or less irregular and sometimes rather strongly angular.

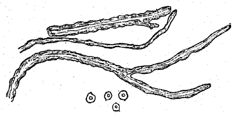


FIG. 2.—Spores and threads of capillitium of *Geaster leptospermus.*

Dr. Coker has furnished me with an interesting note concerning the habitat and collection of the plant, which I append here:

"The plant was first found (a single specimen) by Mr. C. A. Shore, on the trunk of a cedar tree (*Juniperus virginiana*), growing with moss. Since that time I have found it repeatedly (as has also Mr. Shore) sometimes in large numbers (a score or more), and always on the trunks of trees growing with moss. It often occurs in association with *Lycoperdon leprosum* as the same situation is affected by both. The Geaster never grows in close clusters, but the individuals are scattered here and there at varying distances. It seems to grow indifferently on almost any tree where moisture conditions are favorable. I have found it on Ulmus, Hicoria and Juniperus. The mycelium penetrates the old bark and extends itself abundantly between the planes of cleavage."

The species may be described as follows:

Geaster leptospermus Atkinson & Coker, n. sp. Plants occurring singly or gregarious, oval to globose. Peridium 3–4.5 μ in diameter, outer layer closely attached to the moss and bark of the tree by numerous mycelial threads. Outer peridium splitting radially into 3–4 rays, its inner and outer layer then separated by a plane of cleavage, the inner layer being everted, leaving the outer layer in the form of a thin membranous cup with a stellate margin, points of the inner layer remaining attached to the points of the rays of the outer layer, its inner face minutely granular, white or with a flesh colored tinge. Inner peridium sessile or only very slightly pedicellate, 2.5–3.5 μ in diameter, globose and borne aloft by the eversion of the inner layer of the outer peridium, as in other fornicate species of the genus; mouth well defined, not sulcate nor striate, but marked by distinctly radiate silky threads, opening at maturity by a minute perforation; surface whitish or pale lead color, the area about the mouth white. Capillitium abundant, whitish or pale yellowish-brown, extending from the inner surface of the inner peridium towards the center; threads straight or very flexuous and irregular, simple or sometimes branched, 2–6 μ in diameter. Spores very minute, 1.5–2.5 μ in diameter, white or pale yellowish-brown, smooth, that is, not tuberculate nor echinulate, but often irregular and sometimes rather strongly angled, 3–4 angles in side view.

On moss covered dead bark of living trees (*Juniperus virginiana* Hicoria, Ulmus, etc.), woods, Chapel Hill, N. C.— GEORGE F. ATKINSON, *Cornell University, Ithaca, N. Y.*

TILLETIA IN THE CAPSULE OF BRYOPHYTES.

IT has been known for several years that the capsules of certain mosses and liverworts are sometimes attacked by fungous parasites that

fill these structures with a mass of mycelium, which develops small spores as in the Ustilaginales. These spores were first described for Sphagnum by Schimper in 1858 as "microspores," which he supposed to result from the extensive division of the spore mother-cells. Nawaschin, however, in 1892, determined the "microspores" to be derived from a fungus, which he regarded as probably a Tilletia and named *Tilletia* (?) *sphagni.* In the absence of information on the methods of spore germination, the exact position of the fungus must remain uncertain.

Cavers[2] has found a similar fungus in the capsule of *Pallavicinia Lyellii*, whose spores had also previously been called "microspores" by Warnstorf in 1887, and similar conditions were found in *Pallavicinia hibernica*. Cavers, however, presents no details of their structure and development.

The earliest observations on fungous mycelium in the liverworts seem to have been those of Leitgeb on several forms in the Jungermanniales.[3] He determined that the fungus entered the neck of fertilized archegonia and that the infected sporophytes, after a short period of irregular growth, remained abortive, the cavity becoming filled with mycelium in which spores were formed by abstriction.

The most recent contribution to the subject is by H. and P. Sydow[4] who have found this Tilletia-like fungus in the sporophyte of *Anthoceros dichotomus*, and named it *Tilletia* (?) *abscondita.* Nothing is known, however, of the development of this form.

Botanists are probably not generally aware that the liverwort, *Ricciocarpus natans*, harbors a parasite which appears to be similar to this Tilletia (?) described in the other bryophytes. I have repeatedly met it in the preparations of my classes where this liverwort was under observation. The infected capsules fail to mature and the interior becomes filled with small spores. These fungi offer an attractive field for investigation and their life history, completely studied, would clear up a very confused subject.—BRADLEY M. DAVIS, *The University of Chicago.*

[2] CAVERS, On saprophytism and mycorhiza in Hepaticae. New Phytologist **2**: 30. 1903.

[3] Untersuchungen über die Lebermoose 2: —.

[4] SYDOW, H. and P., Die Mikrosporen von *Anthoceros dichotomus* Raddi, *Tilletia abscondita* Syd. nov. spec. Ann. Mycologici **1**: 174–76. 1903.

TWO MEGASPORANGIA IN SELAGINELLA.

(WITH ONE FIGURE)

PROFESSOR BOWER records[5] finding two sporangia subtended by the same sporophyll of *Lycopodium rigidum*. In my work on *Selaginella rupestris* I have recently found two instances of the same irregularity. In both cases they were megasporangia, and were placed not side by

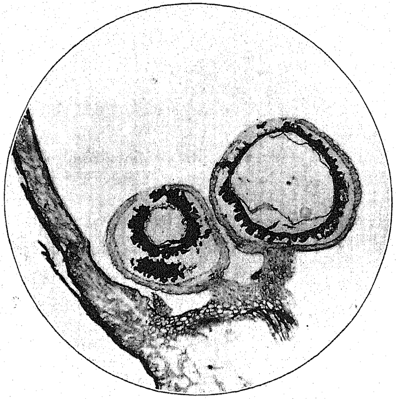


FIG. 1.—Longitudinal section of a megasporophyll of *Selaginella rupestris*, showing two megasporangia in nearly median longitudinal section. From a photomicrograph.

side as in the Lycopodium described by Professor Bower, but as if the additional sporangium was developed in the line connecting the normal megasporangium with the ligule, as shown in the figure. The two sporangia are of equal size, and no smaller than the other sporangia in the same cycle. The figure shows the normal reduction of the megaspores to one or two, so common in *Selaginella rupestris*, as recorded by the writer.[6]—FLORENCE M. LYON, *The University of Chicago*.

[5] BOWER, F. O., Note on abnormal plurality of sporangia in *Lycopodium rigidum* Gmel. Ann. Botany 17: 278-280. 1903.

[6] BOT. GAZ. 32: 138. 1901.

CURRENT LITERATURE.

BOOK REVIEWS.

Morphology of angiosperms.

THIS book,[1] which follows the one on gymnosperms by the same authors, seems a successful accomplishment of the authors' expressed purpose, "to organize the vast amount of scattered material so that it may be available in compact and related form." The want of such a book has long been felt by teachers, and several of the recently published accounts of research in this group make it evident that such a summing up of the facts and literature of the subject has been needed by investigators. The work is not merely a compilation, however, for much of the text, as well as the many pertinent figures credited to the authors, show that they themselves have worked over the subject-matter in many of its important phases.

In the introductory chapter are pointed out the differences between the gymnosperms and angiosperms, which, the authors believe, justify the raising of each of these groups to the rank of a grand division of the vegetable kingdom, as has been done by Warming and others. The close similarity shown by the monocotyledons and dicotyledons is given as sufficient reason for considering both groups together, in the discussion of each detail of development. The reviewer believes that the clearness, so characteristic of the book, could have been further enhanced by a separate treatment of each of these groups.

The discussion of the structure and development of the flower in chapter II is brief, but thoroughly modern, and it will doubtless serve a good purpose in helping to eradicate the older conceptions, still fostered in certain quarters by text-books and floras.

A detailed account of the phenomena of reproduction is given in six chapters (III–IX) with the following headings: microsporangium, megasporangium, female gametophyte, male gametophyte, fertilization, endosperm, and embryo. By the separate treatment of each of these phases of development the discussion gains much in lucidity and in convenience for reference.

The still debatable view of Strasburger that the gametophyte begins with the spore mother-cell, in which the characteristic reduced number of chromosomes first appears, is accepted by the authors. They hold that this view is supported also by the fact that in many temperate perennials the mother-cell stage is the one at which the seasonal rest in development occurs.

[1] COULTER, JOHN MERLE, and CHAMBERLAIN, CHARLES JOSEPH, Morphology of Angiosperms (Morphology of Spermatophytes, Part II). 8vo. pp. vii+348. *figs.* 113. New York: D. Appleton & Co. 1903. $2.50.

The morphological individuality of the megasporangium is insisted upon, and the same claim is made for the sepal, petal, stamen, and carpel.

In the chapter upon the female gametophyte the development of this structure is followed up to fertilization, including the specialization of various parts of the embryo-sac as haustoria. The meaning of the constant occurrence of a definite number of chromosomes in each species is discussed, and also the criterion for distinguishing megaspore from megaspore mother-cell.

The chapter on the male gametophyte deals with the formation and germination of the microspore, and the reduction question. The authors hold that a qualitative reduction of chromosomes is not yet proven. The structures appearing in the pollen grain at germination they believe to represent an antheridium only, of which the pollen tube is the much elongated wall-cell.

In the discussion of fertilization, chalazogamy is thought to be an insufficient evidence of primitiveness. The centrosome is not demonstrated in angiosperms. "Double fertilization" is regarded a misleading name for the process so called, since this and all other nuclear fusions occurring in the embryo-sac probably differ profoundly from the fusion of the male nucleus with that of the egg.

In the chapter on the endosperm the various types of development of the part of the embryo-sac dominated by the endosperm nucleus are described. The endosperm is believed to be a renewed growth of the female gametophyte.

The specialization of parts of the proembryo and embryo for food absorption during development is emphasized in the chapter on the embryo. The characters of the cotyledons, it is held, cannot yet be considered as preponderating evidence in phylogeny. The chapter concludes with an account of parthenogenesis and polyembryony.

The reviewer believes that a valuable addition to the book could be made by following the chapters on endosperm and embryo with a thoroughly modern account of the germination of the seed.

A clear and suggestive résumé of our knowledge, and ignorance, of the interrelationships of the Monocotyledones, Archichlamydeae, and Sympetalae is contained in chapters X, XI, and XII.

Geographical distribution and fossil angiosperms are treated in the two following chapters. There is a concise and very useful summing up here of facts concerning these topics, which have been gathered from sources widely scattered and often inaccessible.

The facts of morphology assume definite relation and proportion only when they are built into some scheme attempting to express the phylogeny of the forms concerned. Such schemes of phylogeny are also the most useful indicators, to the investigator, of the forms most likely to yield important morphological results. If the scheme followed is erroneous, the worker is likely soon to discover the faults of the tool, and the refutation of a wrong

scheme of phylogeny is to be counted a step in advance, even though it be replaced by another imperfect one. The authors are, therefore, quite justified in giving the concise review and criticism of current views of the phylogeny of vascular plants that is to be found in chapter XV. Very important also, in its bearing on this subject, is the presentation of the leading facts of the anatomy of the vascular plants, given in the two concluding chapters of the book by professor Edward C. Jeffrey, of Harvard University.

The well arranged and efficiently complete bibliographies are sure to prove a most valuable feature of the book to investigators. An adequate series of figures has been well selected from many sources, and they are admirably executed, excepting perhaps the never-satisfying photomicrographs of the embryo-sac.—D. S. JOHNSON.

Experimental morphology.

THE LITERATURE of experimental morphology has received an important addition by Dr. Klebs. The present publication[2] is really a continuation of his older work (1896) on the physiology of reproduction in algae and fungi, and carries the theoretical as well as the experimental side of the subject of reproduction and development into higher plants. Beginning with a short history of the development of this branch of botany, from the time of Knight forward, the introduction proceeds with definition and discussion of such subjects as specific structure, causality, external and internal conditions, the teleological point of view, etc. As would be expected, this author does not regard a teleological explanation as any explanation at all. His clear exposition of the purely objective method of interpretation will doubtless be a great help to students who have difficulty in breaking away from the sometime prevalent teleology. His discussion of external and internal conditions is hardly satisfactory, however; one feels that, after all, the division, convenient as it may be, is an arbitrary one. Indeed, to the reviewer it seems as though we might soon be able to discard both terms altogether, naming a stimulus where we have come to know it and confessing ignorance where it is still outside our knowledge. A physiology based on study of the protoplasm can hardly make a distinction between external and internal factors; the cell sap is physiologically as much external to the organism as is the atmospheric air, and the protoplasm itself is probably made up of a number of different systems, often external to one another, and influencing one another in many ways.

Klebs describes several new and instructive experiments with *Ajuga reptans*, *Glechoma hederacea*, *Veronica chamaedrys*, and others. By darkness, rather high temperature, and plenty of moisture, cuttings of the flowering shoot of *Ajuga reptans* were transformed into runners, producing rosettes instead of the normal floral bracts and flowers. Also, a runner submerged in water grows erect to the surface of the medium and then returns to its hori-

[2] KLEBS, G., Willkürliche Entwicklungsänderungen bei Pflanzen. pp. iv + 166. *figs. 28.* Jena: Gustav Fischer. 1903.

zontal habit. Flowering shoots of *Veronica chamaedrys* were made to take the form of an ordinary vegetative shoot by growing them as cuttings in moist air. Many other fascinating experiments are described.

The book is full of suggestive theoretical discussions. In the author's interpretation of these phenomena of higher plants, the responses already obtained in lower plants are taken into account. Thus, the whole manner of treatment is one based on the physiology of the cell itself. On the whole, the work is an admirable one and one which will immediately take its place alongside Dr. Klebs's earlier treatise as among the first to present the subject of development from the standpoint of objective physiology.—BURTON E. LIVINGSTON.

MINOR NOTICES.

THE THIRD PART of Maiden's Revision of the genus Eucalyptus[3] contains text and figures for *Eucalyptus calycogona* Turcz.—C. R. B.

THE SIXTEENTH PART of Engler's *Das Pflanzenreich* includes a conspectus of the families Scheuchzeriaceae, Alismataceae, and Butomaceae by Fr. Buchenau.[4]—C. R. B.

"WITH THE TREES"[5] is the title of a recent book which furnishes evidence of the increasing popular interest in the trees and forests. Such subjects as: When the sap stirs, The life of leaves, The work of leaves, In the high woods, In a hillside pasture, Trees of streets, parks, and gardens, are very interestingly treated by the author. The book indicates a thorough knowledge and familiarity with the botanical problems discussed. The usual tendency of popular writers to personify plants is carried to an extreme in many cases. While this may lend a certain vivacity to the style, the practice is unfortunate, because it conveys erroneous impressions of the life-processes and of the probable origin of structures in plants. The book is very well illustrated from photographs by Edmund H. Lincoln and C. B. Going.—CLIFTON D. HOWE.

THE STUDY of the life-history of truffles has lately engaged the attention of several French investigators. On December 10, 1900, M. Émile Boulanger deposited with the Paris Academy of Science a sealed paper, which was opened at his request on May 4, 1903. It contained a description of his success in germinating the ascospores of *Tuber melanosporum* and *T. uncinatum*. He further described the mycelium, and a conidial stage, and announced

[3] MAIDEN, J. H., A critical revision of the genus Eucalyptus. Part III. pp. 77–90. *pls. 9–12*. Published by the Government of the state of New South Wales. Sydney: W. A. Gullick. 1903. 2*s*. 6*d*.

[4] ENGLER, A., Das Pflanezenreich. Heft 16. Scheuchzeriaceae (pp. 19), Alismataceae (pp. 66), und Butomaceae (pp. 12), von Fr. Buchenau. Leipzig: Wilhelm Engelmann. 1903. *M*. 5.

[5] GOING, MAUD, With the trees. 12mo. pp. x + 335. *figs. 40*. New York: The Baker and Taylor Co. 1903. $1.00.

his plans for cultivation of these species on a considerable scale in the open. M. Louis Matruchot later presented a note to the Academy of Sciences in which he announced for the mycelium of these truffles characters absolutely contrary to those given by M. Boulanger. M. Boulanger has now published a quarto pamphlet,[6] figuring and describing the germination of the ascospores *Tuber melanosporum*, in which he also has reprinted extracts from the proceedings of the Academy of Sciences and the Bulletin of the Mycological Society of France, of various dates. From the description which he gives and the terminology used it would appear that he is absolutely unqualified by a knowledge of the morphology of fungi to discuss the recondite matters upon which he is engaged.—C. R. B.

IN BULLETIN 44 of the Bureau of Plant Industry, von Schrenk and Spaulding[7] give an excellent account of the bitter rot, which is one of the most serious enemies of the apple industry in the middle states. The bulletin deals first with the disease as it appears on the fruit, and later with the canker stage, which is shown to arise from the infection of wounds by spores, and to enable the fungus to live through the winter. Both phases are illustrated by numerous excellent half-tone engravings. The growth of the fungus in cultures is also treated. In describing the germination of the spores the authors follow the error of many other writers in regarding the appressoria as some kind of "chlamydospore."

From the historical review it appears that the bitter rot fungus has been described under various names on grapes, apples, peaches, and nectarines. Recently the ascus-form of several anthracnoses has been discovered. Those species were separated as a genus, *Gnomoniopsis* Stoneman. Since this name had been previously used, the authors propose the name Glomerella[8] for all anthracnoses whose ascus-form is known. The bitter rot fungus, through synonymy, becomes *Glomerella rufomaculans* Spaulding and von Schrenk. The paper concludes with a very comprehensive bibliography.—H. HASSELBRING.

THE SUCCESS of Dr. Grout's little book *Mosses with a hand lens*, has led him to publish a new and larger work,[9] of more extended scope. Even this makes no pretensions to being a complete manual, but is intended rather to attract and help students who would otherwise never begin the study of

[6] BOULANGER, M. ÉMILE, Germination de l'ascospore de la truffe. pp. 20. *pls. 2.* Paris. 1903. Apparently published by the author.

[7] VON SCHRENK, H., and SPAULDING, P., The bitter rot of apples. Bull. no 44. Bureau of Plant Industry. U. S. Dept. of Agric. pp. 54. *pls. 9. figs. 9.* 1903.

[8] Also published in Science N. S. 17:75. O 1903.

[9] GROUT, A. J., Mosses with hand lens and microscope, a non-technical handbook of the more common mosses of the northeastern United States. Part I. Imp. 8vo. pp. i+86. *pls. 10. figs. 35.* Brooklyn, N. Y., 360 Lenox Road: Published by the author. 1903. $1.

mosses. Inasmuch as the diagnostic characters of the species are drawn chiefly from the author's experience, every student of mosses may find the book not only convenient for the ready determination of miscellaneous collections, but even helpful in discriminating critical species. Half of the first part is devoted to directions for collecting, preserving, mounting, methods of manipulation, an account of life history and structure, and an illustrated glossary of bryological terms. The beginning of the manual proper occupies the remainder, with descriptions of Sphagnaceae, Andreaeaceae, Georgiaceae, Polytrichaceae, Buxbaumiaceae, Fissidentaceae, and Dicranaceae. The descriptions of families are rather full, the classification following closely Jameson's *Handbook of British Mosses*, and they are accompanied by numerous illustrations of the characteristic structures. Many of the plates are reproduced from the *Bryologia Europaea*, some from Sullivant's *Icones Muscorum*, while a goodly number of illustrations are original. The book deserves hearty welcome from teachers and students.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS.

ATTENTION SHOULD BE CALLED to an important article by F. Cavers[10] on asexual reproduction and regeneration in Hepaticae. The paper supplements the extensive work of Correns on similar phenomena in the mosses.—C. R. B.

MR. W. C. W[ORSDELL] writes a historical sketch[11] of the phenomenon of "double fertilization" in angiosperms in which most of the literature of the subject is mentioned except the work of American students, and this is conspicuous by its absence.—C. R. B.

DR. EMERICH ZEDERBAUER holds[12] that two of the Myxobacteriaceae described by Thaxter, *Myxococcus incrustans* and *Chondromyces glomeratus*, and probably all members of the group, are compound organisms, like lichens, a true fungus on the one hand in symbiosis with a bacterium on the other. He has grown each component separately in pure cultures and studied their characteristics.—C. R. B.

M. PH. EBERHARDT has made an extended study of the influence of dry air and humid air upon the form and structure of plants.[13] The work was carried on at the botanical laboratory of the Sorbonne and the experimental grounds at Fontainebleau. Plants growing in the ground were covered with

[10] CAVERS, F., Asexual reproduction in Hepaticae. New Phytologist **2**:112–133, 155–165. *figs. 8.* 1903.

[11] W[ORSDELL], W. C., The phenomenon of "double fertilization" in angiosperms; an historical sketch. New Phytologist **2**:145–155. 1903.

[12] ZEDERBAUER, EMERICH, Myxobacteriaceae eine Symbiose zwischen Pilze und Bacterien. Oesterr. Bot. Zeits. **53**:309. 1903.

[13] EBERHARDT, PH., Influence de l'air sec et de l'air humide sur la forme et sur la structure des végétaux. Ann. Sci. Nat. Bot. VIII. **18**:61–153. *pl. 1.* 1903.

bell jars of adequate size, proper arrangements being made for ventilation and for maintaining the moistness or dryness of the air at will. Although the paper contributes few entirely new facts, it brings experimental evidence to bear upon conclusions already drawn from comparative observations.—C. R. B.

SCHIFFNER'S studies[14] of Gymnomitrium and Marsupella may be summarized in the following synonymy: MARSUPELLA SPRUCEI (Limpr.) Bern. *stat.* MARSUPELLA USTULATA Spruce (*Sarcoscyphus Sprucei decipiens* Limpr.; *Nardia gracilis* Mass. & Car.). GYMNOMITRIUM ADUSTUM Nees (*Marsupella olivacea* Spruce; *Acolea brevissima* Dum. inadmiss.). MARSUPELLA CONDENSATA (Angstr.) Kaal. (*Gymnomitrium condensatum* Angstr., *non* Limpr.; *Sarcoscyphus aemulus* Limpr., *et auct.*) MARSUPELLA (*Hyalacme*) APICULATA Schiffn. (*Gymnomitrium condensatum* Limpr. *et auct.*, *non* Angstr.). GYMNOMITRIUM ALPINUM (Gott.) Schiffn. (*Sarcoscyphus alpinus* Gott.)

BY USING MODERN METHODS in an investigation of the development of the antheridial "flower" of Polytrichum and Mnium, Vaupel seems to have settled the Hofmeister-Leitgeb-Goebel controversy as to its morphology.[15] In Mnium each cluster of antheridia in the "compound male flower" (*i. e.*, each twig of the branch system) corresponds to the antheridial group of Funaria, in that the first antheridium develops from the apical cell, the rest arising at various points. Leaf formation in the center of the "flower," however, is suppressed, all the segments forming antheridia. But in Polytrichum the apical cells of the twigs do not produce antheridia, persisting even until rudiments of the last antheridia appear. Thus again the truth lies between the contestants. Vaupel also ascertained that the brown substance in certain cells of the paraphyses of *Mnium cuspidatum* and *Polytrichum juniperinum* prevents the absorption of water by the stems, leaving it all to the antheridia; that the opening of the antheridia of Marchantia is due to the swelling of the mucilage laid down in the wall cells; and that the rhizoid strands of Polytrichum are primarily water conductors.—C. R. B.

RESPIRATION.—Further researches on the influence of injuries upon the respiratory quotient have been made by Maximow,[16] who corrects some of Richards's results, confirms others, and concludes that (1) the variations are due partly to the capacity of fleshy organs to retain for a time considerable amounts of CO_2 and to eliminate it later in excess; (2) when injured the early increase of CO_2 (which soon ceases) is due to the exposure of additional

[14] SCHIFFNER, VICTOR, Studien über kritische Arten der Gattung Gymnomitrium und Marsupella. Oesterr. Bot. Zeits. 53:95–99, 166–172, 185–194, 246–252, 280–284. *pls. 2–4.* 1903.

[15] VAUPEL, F., Beiträge zur Kenntniss einiger Bryophyten. Flora 92:346–370. 1903.

[16] MAXIMOW, N. A., Ueber den Einfluss der Verletzungen auf die Respirationsquotient. Ber. Deutsch. Bot. Gesells. 21:252–259. 1903.

free surface; (3) the value of the respiratory quotient then falls rapidly, sometimes as low as 0.5, reaching a minimum before respiratory activity attains its maximum, which it does on the second or third day; (4) with healing, normal conditions again gradually prevail.

NABOKICH confirms[17] earlier results of Polowzoff[18] that a considerable part (25–50 per cent. of the CO_2 usually ascribed to the respiration of seeds in experiments is really due to the respiration of microorganisms, as shown by a comparison of the respiration of sterile and infected seeds. He also ascertained that the antiseptics used (bromin and corrosive sublimate) did not depress the respiration of the seeds, but clearly accelerated it.—C. R. B.

[17] NABOKICH, A. J., Ueber den Einfluss der Sterilisation der Samen auf die Athmung. Ber. Deutsch. Gesells. **21**:279–291. 1903.

[18] POLOWZOFF, W. W., Untersuchungen über die Athmung der Pflanzen. Ber. Kaiserl. Akad. Wiss. VIII. **12**:14–16. 1903.

NEWS.

DR. WILLIAM TRELEASE spent a month in Mexico this summer in the study of agaves and other plants.

DR. O. MELVILLE BALL, of Batesville, Va., and DR. E. F. FRITSCH, of London, have been elected members of the German Botanical Society.

MR. W. BOTTING HEMSLEY, keeper of the Kew Herbarium, has been made associate editor (with Sir Joseph Hooker) of the *Botanical Magazine.*

THE BOTANICAL DEPARTMENT of Stanford University has just entered the new and commodious quarters which have been in process of construction for more than three years.

DR. J. A. HARRIS, of the Missouri Botanical Garden, has been appointed assistant in the Shaw School of Botany of Washington University. An appointment of his successor at the Garden will shortly be made.

MR. CHARLES A. DAVIS, instructor in forestry in the University of Michigan, is engaged in an extended comparative study of the inland lakes and bogs of the lower peninsula of the state with reference to their geological and botanical history and the conditions of peat formation.

PROFESSOR CHARLES E. BESSEY has been accompanying his son this summer in a journey through the Caucasus region. They crossed the mountains by the Mamisson pass—"a botanist's paradise," he writes—and were in Tiflis on August 19. After a week's journey to the south, they were to turn homeward.

MR. FILBERT ROTH, recently appointed to the chair of forestry in the University of Michigan, has also been elected forest warden of the state by the Michigan Forestry Commission. He has organized a party of forestry students, who are engaged in a preliminary survey of the state forest reservations in Roscommon county, Michigan.

WE LEARN from the *Journal of Botany* that the second and third volumes of the *Icones ad Floram Europae*, including plates 281–500, have been issued under the superintendence of M. Camille A. Jordan, the text having been prepared by the late Alexis Jordan. The remaining incomplete text and about 100 plates will not be published, but have been intrusted to the Botanical Society of France, at whose rooms they may be consulted.

DR. D. H. CAMPBELL left San Francisco on May 15, spent three weeks in New Zealand, and a month in Australia, where, through the kindness of Mr. Maiden, the director of the Sydney Gardens, he saw a great deal of the very

characteristic flora of the country, going as far as Melbourne and a little north of Brisbane, besides making a number of shorter excursions. On the the way back he was two weeks in Hawaii, returning to Stanford University September 1.

DR. HERMAN VON SCHRENK, whose government work has been growing constantly, withdraws from the School of Botany of Washington University to give all of his time to the work in plant pathology and the preservation of timbers for the Department of Agriculture, with the title of Chief of the Division of Forest Products, under the Bureau of Forestry. He continues in charge of the Mississippi Valley Laboratory of the Bureau of Plant Industry, located at the Missouri Botanical Garden.

A GARDEN OF MEDICINAL PLANTS is to be established at Golden Gate Park, San Francisco, Cal. The park commissioners have set aside eight acres of ground in a well protected part of the park and have instructed the park superintendent and the authorities of the California College of Pharmacy to further the plans of such a garden. Climatic and other conditions are exceptionally favorable, and it is believed that fully 90 per cent. of all medicinal plants may be grown in the open. Others will be cared for in greenhouses.

AT THE UNIVERSITY OF IOWA: Men have been in the field all the year making collections to complete as far as possible the herbarium representing the state flora. Collections have been made chiefly in the northeastern and in the southern counties of the state. PROFESSORS MACBRIDE and SHIMEK have just returned from an excursion down the valley of the Rio Grande. They bring back large collections both of cryptogamic and flowering plants, besides a very large number of photographs representing the ecological conditions of mountain and plain, forest and desert.

AT THE UNIVERSITY OF CALIFORNIA: PROFESSOR W. A. SETCHELL is spending his sabbatical year in journeying around the world. His time is to be devoted mainly to botanical sightseeing.

PROFESSOR W. L. JEPSON, who is acting head of the department of botany in the absence of Professor Setchell, has devoted the last two summers to a field study of the forests of northwestern California, centering his investigations particularly on the tan oak and the tanbark industry.

Mr. H. M. HALL, who has charge of the herbarium, which now contains 50,000 sheets, made a wagon journey this summer through the cañon of the upper Sacramento River, circled Mount Shasta, crossed the Modoc lava beds, passed south to Larsen Peak, and threaded the Sierra Nevada Mountains to the Tahoe region and the Calaveras grove. It was a long and very productive journey.

SIR THOMAS HANBURY has presented to the Royal Horticultural Society of London a tract known as Wisley Garden, situated twenty miles from Hyde Park Corner. The *Gardener's Chronicle* reports it as "unique . . . . devoid

of all plan and in all its aspects as wild as a garden can be . . . . It was made piecemeal and as the late Mr. Wilson's fancy dictated. . . . . There are no broad paths . . . . no geometrical beds. . . . . All is natural, yet natural with plants of every conceivable description. . . . . Not a thing is named, but labels in such a garden, if used, must be numbered by thousands. . . . . There is no digging permitted in the many acres thus wildly planted. The men do little else but pull weeds, and occasionally use the knife." It is to be hoped that the garden will be maintained as at present and that the Society will reorganize its garden at Chiswick and equip it with a staff of investigators for experimental work.

NOTES FROM THE BUREAU OF PLANT INDUSTRY OF THE U. S. DEPARTMENT OF AGRICULTURE:

DR. GEORGE T. MOORE, physiologist, has been sent to Europe for the purpose of investigating the methods used there in the study of soil bacteriology, and for the purpose of securing plants of various kinds for the Office of Seed and Plant Introduction. He will return in January.

MR. W. T. SWINGLE has just returned from the Mediterranean region, after an extended study of the pistache, a nut-bearing tree which the department is introducing into the southwest. Mr. Swingle has also made a careful study of several other Mediterranean crop plants and fruit trees, which the department is proposing to introduce into the same region. He will remain in Washington for some time.

MR. P. H. DORSETT has been authorized to establish in some portion of southern California a plant testing and acclimatization garden, in cooperation with the Agricultural Experiment Station of California. This garden will be used to test and propagate rare and valuable plants introduced by the department. MR. W. W. TRACY will assist Mr. Dorsett in selecting the location, which will be announced soon.

MR. W. M. SCOTT, late state entomologist of Georgia, will give his attention especially to work on the diseases of orchard fruits.

A NUMBER of scientific assistants and aids have recently been appointed. In the Office of Physiological and Pathological Investigations: P. J. O'GARA, GEORGE F. MILLS, LEONARD F. HARTER, of Nebraska, and ARTHUR H. LEIDIGH, of Kansas. Mr. O'Gara and Mr. Harter will be stationed in Washington, and Mr. Leidigh at Amarillo, Texas, on one of the government experiment farms. In the office of the agrostologist: M. A. CROSBY, and M. B. STEVENS, of Michigan; BYRON HUNTER, of Washington; R. A. OAKLEY, of Kansas; C. W. WARBURTON, of Iowa.

MR. W. J. SPILLMAN is investigating forage conditions in the northwest. C. R. BALL and DAVID GRIFFITHS are also in the field, the former in connection with the exhibits at St. Louis, and the latter studying range problems in the southwest.

MR. A. S. HITCHCOCK has returned from a three-months' trip from Louisiana to California and Washington, where he has been investigating

agricultural conditions, and the methods for preventing the drifting of sand in sand-dune areas. MR. J. M. WESTGATE, a graduate of the Kansas Agricultural College and later a student in the botanical department of the University of Chicago, has been appointed an assistant in this work.

MR. C. V. PIPER, professor of botany in the Washington Agricultural College, has been appointed systematic agrostologist in charge of the herbarium of grasses.

PROFESSOR L. H. BOLLEY is still in Russia, studying varieties of flax with a view to introducing desirable kinds into the United States. He will return about November 1.

MR. J. E. W. TRACY is in Europe studying the seed-growing industry. He will make himself familiar with the methods of the best growers and with the most desirable new European varieties of vegetables.

THERE WILL soon be published as a bulletin a paper entitled "Conditions influencing the vitality and germination of seeds," by DR. J. W. T. DUVEL. It is a historical review of the work already done on the vitality of seeds, as well as a report of the results of his own investigations carried on at the University of Michigan in 1900, 1901, and 1902.

MR. ERNST BESSEY is at present in the Caucasus making observations on such of the native fruits and nuts as may seem valuable, and will send seeds and plants to the United States.

MR. GEORGE OLIVER has just returned from Florida, where he studied the mango culture with a view to the further introduction of choice varieties.

MR. BARBOUR LATHROP, of Chicago, who has made several expeditions at his own expense to different parts of the world, in search of valuable seeds and plants for introduction into America, has just returned. He has employed on his various expeditions MR. D. G. FAIRCHILD, who now resumes his connection with the department as one of its agricultural explorers. The countries visited this year with a view to more thorough exploration later by the department agents were Italy, Sicily, Tripoli, Tunis, Malta, Egypt, German East Africa, Zanzibar, Portuguese East Africa, Natal, Transvaal, Cape Colony, Grand Canary, Madeira, Portugal, Spain, Bohemia, Sweden, Denmark, Holland, Belgium, and England. Such seeds and plants as were secured were given by Mr. Lathrop to the Department of Agriculture for propagation and distribution, and it is hoped that some of them may prove of great value to the country, repaying him for his patriotic and generous interest in increasing the variety of food and ornamental plants of America.

VOLUME XXXVI NUMBER 5

BOTANICAL GAZETTE

NOVEMBER, 1903

ODONTOSCHISMA MACOUNII AND ITS NORTH AMERICAN ALLIES.

ALEXANDER W. EVANS.

(WITH PLATES XVIII–XX)

HISTORICAL.

AMONG the hepaticae recently collected by Professor John Macoun in the Yukon Territory are several fruiting specimens of *Odontoschisma Macounii*, a species confined to the higher latitudes and hitherto known in sterile condition only. The species has had a rather varied history. It was first described by Austin,[1] in 1872, as *Sphagnoecetis Macounii*, the original specimens having been collected in the Lake Superior region of Ontario in 1869. A portion of this original material has been kindly furnished me by Professor Macoun, but unfortunately it does not appear to be altogether homogeneous. Some of the specimens are gemmiparous and are pale green in color, while others are without gemmae and are more or less tinged with yellow or brown. It is evident that Austin's description is drawn almost entirely from the pale specimens, which may therefore be regarded as the type of the species. It is very probable also that the darker specimens are not specifically distinct from the others, and that their coloration is due simply to exposure to the sun. Nevertheless, on account of their incomplete character, this question can hardly be settled definitely at present. *O. Macounii* is either mentioned or briefly described by Underwood,[2] by Pearson,[3] and by

[1] Bull. Torrey Bot. Club 3: 13. 1872.

[2] Bull. Illinois State Lab. Nat. Hist. 2: 92. 1884. BOT. GAZ. 17: 312. 1892.

[3] List of Canadian Hepaticae 10. 1890.

Macoun,[4] but there is apparently no printed record of its having been collected a second time.

In the writings of certain Scandinavian bryologists, however, are a few references to a small arctic hepatic which agrees closely with the pale type specimens of *O. Macounii* and which is doubtless referable to Austin's species. This plant was first collected by Berggren in 1868 at King Bay on the island of Spitzbergen, and was described by him in 1875 under the name *Sphagnoecetis communis* var. *tessellata*.[5] In a second paper, also published in 1875,[6] he recorded the plant from Disco Bay on the western coast of Greenland, where he had collected it five years previously. This time it appears as *Jungermannia tessellata*, showing that he was not altogether certain as to its systematic position. Under this latter name the Greenland specimens are mentioned by Lange and C. Jensen[7] in 1887, and by Underwood[8] in 1892. In 1898 Kaalaas[9] recorded the species from Norway; he recognized in it an Odontoschisma, but referred it, as Berggren orginally did, as a var. *tessellata* to *O. Sphagni*. In the same year C. Jensen[10] published excellent figures of the plant under the name *O. tessellatum*. The specimens from which his figures were drawn were collected by Hartz at Scoresby Sound, on the eastern coast of Greenland, well within the Arctic Circle. Herr Jensen has kindly sent me two East Greenland specimens of his *O. tessellatum*, which were collected by Dusén in 1899,[11] and I have also been able to study Norwegian specimens collected and communicated by Herr Jörgensen. These specimens have served for comparison with Austin's type of *O. Macounii*. Additional specimens from Yukon, collected by Williams, and from northern Minnesota, collected by Holzinger, have also been examined. It is clearly seen, therefore, that the geographical distribution of *O. Macounii* is much more extensive than the published records would seem to indicate.

[4] Cat. Canadian Plants 7:32. 1902.

[5] Kongl. Sv. Vet. Akad. Handl. 13^7: 101. 1875.

[6] *L. c.* 13^8: 43. 1875.

[7] Meddel. om Grønland 3: 411. 1887.

[8] BOT. GAZ. 17: 311. 1892.

[9] Vidensk. Skrift. I. 1898^9: 14.

[10] Meddel. om Grønland 15: 369. *f. 1–4*. 1898.

[11] *Cf.* C. JENSEN, Öfvers. k. Vetensk.-Akad. Förh. 57: 797. 1900.

Closely related to *O. Macounii*, but differing from it in several important respects, is a peculiar Odontoschisma which was collected by Miss Gertrude Gibbs at Port Renfrew, Vancouver Island, in 1901. This species is apparently undescribed and may be designated *O. Gibbsiae* in honor of its discoverer. The specimens are without sexual organs, but show well developed gemmiparous branches.

Two other members of the genus, *O. denudatum* and *O. Sphagni*, have been recorded from North America, north of Mexico. Both of these species have long been known in Europe, and *O. denudatum* has been reported from Siberia and from Japan. The range of this species in North America extends from Greenland to Louisiana, with a doubtful extension into the tropics. According to printed reports, the range of *O. Sphagni* is even more extensive, but a comparison of authentic European material with American specimens which have been determined as *O. Sphagni* shows that the majority of the latter are really referable to *O. prostratum*, a species originally described from Jamaica. In fact, I have seen no specimens whatever of true *O. Sphagni* from the United States, although the species occurs in Canada. Mitten reports[12] *O. prostratum* from Bermuda, and says that it also occurs in Europe, but the latter statement does not appear to be confirmed by any other European writer. In addition to Jamaica, *O. prostratum* has been reported from several localities in tropical America.

A careful study of these five species makes it evident that certain of the generic characters commonly accepted for Odontoschisma do not apply to all of the species, and that the genus as a whole is about as closely related to the monotypic Anomoclada, of South America, as it is to Cephalozia, with which it is commonly associated.

Odontoschisma was first proposed by Dumortier, in 1831,[13] as a section of his genus Pleuroschisma. This included also, as sections, Lepidozia and Pleuroschismotypus, the latter being essentially the same as Bazzania. In 1835[14] he raised all three

[12] Challenger Rept. Botany 1^2: 92. 1884.

[13] Syll. Jung. 68. 1831.

[14] Recueil d'Obs. sur les Jung. 19. 1835.

sections to generic rank, the section Pleuroschismotypus becoming the genus Pleuroschisma in its restricted sense. Two species of Odontoschisma, *O. Sphagni* and *O. denudatum*, are recognized. In the Synopsis Hepaticarum Nees von Esenbeck[15] redescribed the genus under the name Sphagnoecetis. He recognized but a single European species, *S. communis*, which was made to include both of Dumortier's species. Two exotic species, however, are doubtfully referred to the genus, and three other exotic species are added in the appendix.

In 1874 Lindberg[16] revised the European species of Odontoschisma and clearly distinguished between *O. Sphagni* and *O. denudatum*. Unfortunately he included in the genus *Jungermannia decipiens* Hook., a species which Mitten had placed in his genus Adelanthus[17] (now Adelocolea). In his paper on Anomoclada, published two years later, Spruce[18] showed clearly why Adelanthus should not be included in Odontoschisma. At the same time he fully described the two European species of the latter genus and ascribed to both a very wide geographical distribution, extending, in fact, into the tropics of South America. In 1877 Trevisan[19] accepted the genus Odontoschisma in Lindberg's wide sense, and included in it eleven species, most of them exotic.

In 1882 Spruce[20] reduced Odontoschisma to a subgenus under Cephalozia, on account of the close resemblance between their sexual branches and sporophytes, and he continued so to regard it during the remainder of his life. He was followed in this by Lindberg and by Arnell, as well as by Pearson and by several other hepaticologists of the English school. On the continent, however, and in America, this extreme view has never met with much favor, and Schiffner, in his treatment of the Hepaticae for Engler and Prantl's *Die natürlichen Pflanzenfamilien*, published in 1893, restored Odontoschisma to generic rank. Schiffner estimates the number of species of Odontoschisma at thirteen, and very few additions have been made up to the present time.

[15] G. L. & N. Syn. Hep. 148. 1845.

[16] Notis. ur Sällsk. pro F. et Fl. Fenn. Förhandl. 13:357. 1874.

[17] Jour. Linn. Soc. Bot. 7:244. 1864.

[18] Jour. Bot. 5:166. 1876.

[19] Mem. R. Ist. Lomb. III. 4:418. 1877.

[20] On Cephalozia 59. 1882.

GENERIC CHARACTERS.

The generic characters ascribed by Schiffner to Odontoschisma are those accepted by the majority of recent writers, whether they regard the group as a genus or merely as a subgenus under Cephalozia. The most important of these characters are the following:

Plants rather large, growing in tufts, varying from green to red or dark brown; stems creeping, radicelliferous, not arising from a rhizome; branching uniformly postical; leaves succubous, entire, obliquely or longitudinally inserted, varying in outline from orbicular to ovate, rarely emarginate at the apex, cell walls thickened; underleaves small; ♀ inflorescence on a short branch; perianth hypogonianthous, dentate or ciliate at the contracted mouth; capsule oval.

All of these characters apply pretty definitely to *O. Sphagni* and also to *O. prostratum.* In our other species, however, the branching exhibits considerable variation, especially in *O. Macounii.* In this species, moreover, the mouth of the perianth is entire or nearly so, and the underleaves often attain a considerable size. Underleaves, in fact may be demonstrated in all our species, and although they are sometimes small and transitory in their nature, they afford nevertheless differential characters of considerable importance.

BRANCHING.

The branching in Odontoschisma is always intercalary in character, using this term in the sense suggested by Leitgeb.[21] According to this author, intercalary branches arise almost invariably from the postical segments of an axis. This origin is seen very clearly in Kantia and in the typical species of Cephalozia. It is also seen in the flagella and in the sexual branches of Bazzania. In Odontoschisma the postical origin of the branches may be demonstrated in the normal flagella of all our species (*fig. 44*) and also in the vegetative and sexual branches of *O. Sphagni* and *O. prostratum* (*fig. 42*). In *O. Macounii*, however, the leafy branches and also the sexual

[21] Unters. über Lebermoose 2:21. 1875.

branches are sometimes postical, sometimes lateral (*fig. 1*), and sometimes occupy a position between postical and lateral. In fact, the lateral position is the most frequent and is almost invariably assumed by the sexual branches. In *O. Gibbsiae* and in *O. denudatum*, as well as in the recently described *O. cavifolium* Steph.[22] of Japan, lateral branches are also of occasional occurrence. That the origin of these branches is really postical and their lateral position is due merely to displacement, as Leitgeb maintains is the case in Plagiochila, is not improbable, but it has not been determined with certainty. It is clear, however, that this theory of displacement from the postical segment cannot apply to the genus Anomoclada, where all the branches except the flagella are distinctly antical in position. In this genus it is perfectly apparent that the branches arise from the lateral segments, and the difference in position between such an antical branch and the lateral branches in *Odonotoschisma Macounii* is really not very great.

The lateral branching which occurs in *Cephalozia Turneri* and in some of its immediate allies was used by Spruce[23] as the essential character of his subgenus Prionolobus, a group which Schiffner has since raised to generic rank. On the same grounds *O. Macounii* might be separated generically from *O. Sphagni*, but such a separation would be very artificial, especially when we take into consideration the inconstancy in the position of the branches in *O. Macounii*. In fact, the generic claims of Prionolobus are not above criticism, on account of the occurrence of both postical and lateral branches in certain undisputed species of Cephalozia.

It is probable that the position occupied by intercalary branches, and especially by those of adventitious origin (*i. e.*, by those arising from differentiated axis-cells which have reassumed an embryonic character), is largely influenced by the conditions under which a species develops. This statement would apply especially to plastic species, of which *O. Macounii* seems to offer an example, but it would also apply to the plastic ancestors of

[22] Bull. de l'Herb. Boissier 5:102. 1897.

[23] Hep. Amaz. et And. 508 (footnote). 1885.

forms in which the branching has now become constant. It is clear, for example, that in a species with prostrate stems the postical position of the flagella is of distinct advantage, because it enables these organs at once to penetrate the substratum and to act as fixing and absorbing organs. In a leafy branch, however, the advantages of a postical origin is not so clear. Except at the very beginning, when the branch needs protection from drying, it would be placed at a disadvantage, because it would have to grow out beyond the leaves of the axis before it could develop normally and expose its leaves to the light. In such a case a lateral displacement would enable it to perform its functions earlier, while an antical position would be most advantageous of all. The last, however, would be precarious, unless there were some provision for keeping the branch-rudiment moist; this is secured in Anomoclada by a copious secretion of slime. In sexual branches the postical position is at first of distinct advantage, because it protects the antheridia and archegonia from drying, and at the same time tends to insure fertilization. It continues to be of advantage in such genera as Kantia, where a subterranean sac is developed. But in most cases the female branch curves upward and the perianth shortly assumes a position at right angles to the substratum. In this way the young capsule is so placed that a simple elongation of its stalk will push it above the perianth and expose its ripened spores to currents of air. The latter advantage is, of course, more easily secured by lateral or antical branches. Lateral branching, on the whole, seems to be the most serviceable type. This is seen especially well in the large and very successful group of the Jubuloideae, where postical branching has entirely disappeared. In this group, to be sure, the branching is terminal, and the lateral branches are therefore laid down at the growing apex. There is little doubt, however, that in the ancestors of these forms the method of branching was less definite.

LEAF-CELLS.

The thickening of the cell wall has already been quoted as an important generic character of Odontoschisma, and the variations in the thickening afford excellent differential characters for the

species. The thickening may be observed in the cells of the stems and branches, but is best studied in the leaves. Here it is most pronounced in the angles of the cells, where it forms distinct and often conspicuous trigones, but it affects the cuticle of the leaves as well. In this region the thickening is fairly uniform, and we sometimes find a uniform thickening also in the vertical walls of the marginal cells. Intermediate thickenings seem never to be present.

In *O. Macounii* the thickenings of the cell wall are especially pronounced, the trigones being extremely large, and the cuticle thickened in a corresponding degree (*figs. 5, 6*). The trigones, in fact, project far out into the cell cavities, which become in consequence distinctly stellate with narrow rays, the latter of course forming pits for communication between adjoining cells. It is often possible to recognize in a trigone a distinct line of demarcation separating the original trigone, as laid down in the developing leaf, from a secondary deposit. This line of demarcation is clearly brought out by treatment with sulfuric acid in the presence of iodin, which serves at the same time to demonstrate the presence of cellulose in the wall. The trigones of this species are especially likely to be confluent; in some cases this is true of the original trigones; in other cases the coalescence is brought about by the secondary deposit, which causes at the same time the obliteration of a pit. Much of the thickening of the cuticle is also due to the secondary deposit. The cells of the underleaves are sometimes rather thin-walled, and sometimes have thicker walls than the leaves themselves (*fig. 13*). The last is true also of the leaves on gemmiparous branches, of the perigonial and perichaetial bracts, and of the lower part of the perianth (*fig. 23*). In most of these regions there is a tendency for the cells to be arranged in longitudinal rows, and the excessive thickening brings about an extensive coalescence of trigones. These are commonly united in such a way that the pits connecting the cells laterally are filled up by the secondary deposit, while those connecting the cells longitudinally are retained. Through this process the lower part of the perianth becomes a series of flattened thick-walled tubes, which are continuous except

for the thin partitions separating the cells of which they are composed. These tubes are bounded without and within by the thickened cuticle, and are separated from one another by the coalescent trigones. In the upper part of the perianth the cells are uniformly and only slightly thickened (*fig. 24*), and there is a gradual transition from these to the thick-walled cells just described. The thickenings of the cell walls, although found in all the specimens of *O. Macounii* examined, are especially pronounced in those from the far north.

If we confine our attention to the median leaf-cells, our five species of Odontoschisma will be found to exhibit a regular descending series with respect to their trigones. *O. Macounii* stands at the beginning of this series. In *O. Gibbsiae*, which comes next, the trigones are still large, and the cavities are stellate, but the pits are broader and the trigones are less frequently confluent (*fig. 31*). In this species the trigones rarely show a line of demarcation, except when the portion lining the cavity becomes pigmented, and they also fail to respond directly to the cellulose test. In *O. denudatum* the trigones are still pronounced, but the cavities are less distinctly stellate, the trigones not projecting far enough out into the cavities to leave narrow pits (*fig. 35*). In *O. Sphagni* the trigones are smaller and project only slightly into the cavities, which in consequence become rounded in outline (*fig. 39*). In *O. prostratum* the trigones are still less conspicuous and commonly turn a concave face toward the cavity, which acquires in this way a polygonal outline with rounded angles (*figs. 55, 56*).

Throughout the genus Odontoschisma the median leaf-cells, if we consider them bounded by their middle lamellae, are polygonal in outline and isodiametric. The marginal leaf-cells, however, are quadrate or rectangular in outline, and in the latter case the long axis of the cell is commonly at right angles to the margin. In most species the marginal cells are not very different from the median cells, except for this slight difference in shape. This is true of *O. Macounii*, *O. Gibbsiae*, and *O. denudatum* (*figs. 7, 32, 36*). In other species there are several successive rows of four-sided cells, forming a distinct border around a considerable

portion of the leaf. This bordered appearance is often made more conspicuous by the involute character of the leaf margin. A border of this sort has long been emphasized as one of the most important characters separating *O. Sphagni* from *O. denudatum*. The border of *O. Sphagni* (*fig. 40*), however, is much less distinct than that of *O. prostratum* (*figs. 57, 58*). In both species we find two to four rows of marginal cells which exhibit a tendency, sometimes very clearly marked, to be arranged in radial rows as well. These marginal cells have uniformly thickened walls, giving them a very different appearance from the thin-walled median cells with their small trigones. In *O. prostratum* the leaves exhibit considerable variation, not only with respect to the width of the border, but also with respect to the thickness of the walls of the marginal cells, and the two extreme conditions represented in the figures are connected by a series of intermediate forms. Both in this species and in *O. Sphagni*, the border is indistinct in poorly developed individuals.

UNDERLEAVES.

The underleaves of Odontoschisma present peculiarities which have been strangely overlooked by writers on the genus. In the specimens of *O. Macounii* from Greenland and Yukon, these underleaves are especially large and persistent even on sterile stems, although they are considerably smaller on Minnesota specimens of the same species. Their most remarkable feature is found in the slime-secreting papillae which are borne in large numbers on their margins. Similar papillae are found on the underleaves of our other species of Odontochisma, but they are usually shorter-lived than in *O. Macounii*.

Leitgeb and others have already called attention to the frequent occurrence of papillae in connection with the growing-points of the Hepaticae. In the Jungermanniaceae they seem to be almost constantly present, but are usually restricted to the postical segments cut off from the apical cell. Leitgeb designates these papillae as "primordial," and looks upon them as structures which the leafy hepatics have inherited from their thallose ancestors.[24] When the postical segment is cut off in

[24] Unters. über Lebermoose 2:7 ff. 1875.

these leafy forms, it divides by a periclinal wall into an inner and an outer cell, of which the latter gives rise to the papillae. In some cases this outer cell forms a single papilla before dividing. This is true, for example, of *Cephalozia bicuspidata*, *Nardia hyalina*, and *N. scalaris*. In other cases the outer cell divides by anticlinal walls into two, three, or four cells, each of which gives rise to a papilla. In *Plagiochila asplenioides*, for example, two papillae are formed; in *Acromastigum integrifolium*,[25] three; and in *Bazzania trilobata*, four. In a few species without underleaves, such as *Radula complanata* and *Cololejeunea calcarea*, no primordial papillae are formed by the ventral segments; but, on the other hand, the mere presence of papillae by no means insures the development of underleaves. When the latter are to be formed the papillae elongate, cells are cut off from their bases, and these cells by irregular divisions, both longitudinal and transverse, give rise to the permanent cells of the underleaves. In some cases there are as many lobes or divisions to the underleaf as there are primordial papillae, but usually the portions developing from the different papillae coalesce throughout more or less of their extent, and in some cases this coalescence extends to the very apex of the underleaf, which becomes thereby truncate or rounded.

In all our species of Odontoschisma two primordial papillae are formed and are succeeded by well developed underleaves. In *O. Sphagni* these are unfortunately short-lived, and the species has been described as being without underleaves or as having them rare and minute. As a matter of fact, they are always easy to demonstrate both in this species and in *O. Gibbsiae* near the apex of a vegetative branch, and in our other species they can usually be detected in the older parts of a plant as well. With regard to their structure and development two types of underleaf may be recognized. The first is found in *O. prostratum* and *O. Sphagni*, the other in our remaining three species. In the first type, through a succession of transverse walls in the cells cut off at the base of the papillae, two rows of cells are formed, growth and division continuing for some time at the

[25] EVANS, Bull. Torr. Bot. Club 27: 100. *pl. 1.* 1900.

base of the underleaf. These two rows of cells separate slightly at their free ends, which are tipped with the papillae, but coalesce throughout the greater part of their length. In this way a linear underleaf is formed, slightly bifid at the apex. In *O. prostratum* (*figs. 59–62*) a few longitudinal (or oblique) divisions sometimes occur near the base, and in *O. Sphagni* (*fig. 41*) these divisions are more frequent. Through these longitudinal divisions an underleaf may acquire a subulate form, but it is always much longer than broad. In the second type of underleaf the development begins in the same way, but the order of cell division is much less regular, longitudinal divisions tending to set in very early. The adult underleaves in consequence vary greatly in form, being sometimes distinctly bifid and sometimes rounded or truncate at the apex. In many cases the breadth equals or exceeds the length. These variations affect the underleaves, whether they remain small, as in *O. Gibbsiae* (*figs. 33, 34*), *O. denudatum* (*figs. 37, 38*), and some forms of *O. Macounii* (*figs. 9, 11, 12*), or attain a considerable size, as in the other forms of this same species (*fig. 10*).

As the underleaves develop, some or all of their cells give rise to a series of slime-secreting papillae, similar in all respects to the primordial papillae. In a young underleaf these may be found in all stages of development. A papilla begins as an outgrowth from a cell and soon becomes swollen at its extremity. In most cases a wall is formed at the base of the papilla, cutting it off from the cell. In rare cases this wall is suppressed and the cell simply forms a part of the papilla. Usually the papillae are limited to the margin of an underleaf, but occasionally they grow out from the postical surface as well. This is frequently the case in *O. Sphagni*, where it may even be difficult to distinguish the permanent cells of the underleaf on account of the crowded papillae which cover them. In our other species one or two papillae may occasionally be found on the postical surface. In rather rare cases two papillae may grow out from a single cell. The later development of the papillae has been briefly described by Goebel [26] for *Calobryum Blumei*. A layer of

[26] Ann. Jard. Buitenzorg 9: 15. 1891.

cellulose is deposited within the cell-wall at the swollen extremity of the papilla. Between this layer and the original wall the secretion of slime appears and is set free by the rupture of the wall. In most cases the papillae are short-lived and soon shrivel away. Occasionally, however, there are very clear indications that they continue active for a considerable period. In *O. Macounii*, for example, pits may be demonstrated in the marginal cells of the underleaves, connecting them with the papillae (*fig. 13*), and these pits are especially striking in cases where the cell walls are strongly thickened.

In the case of *O. Macounii*, slime-papillae are not confined to the underleaves. They may also be found on the leaf-margins close to the postical base, on the margins of the perichaetial bracts and bracteoles (*figs. 14–22*), and on short hair-like paraphyllia which are sometimes developed in connection with the archegonia (*fig. 4*). Whenever they occur in any of these localities they appear to be fully as persistent as on the underleaves.

Leitgeb has briefly alluded to the fact that the underleaves of *Bazzania trilobata*, as well as those of certain other species, sometimes bear a few papillae in addition to those which he designates as primordial, but he neither figures nor describes them further.[27] He also calls attention to the occasional occurrence of similar papillae on leaf-margins in more or less indefinite positions. These he would distinguish from primordial papillae, because they develop from leaf-cells (or underleaf-cells) instead of directly from the segments cut off from the apical cell. Although this distinction may be of theoretical interest, it is really of little practical importance, because all the papillae, whatever their origin, have the same structure and functions.

THE FEMALE BRANCH.

The female branch in Odontoschisma affords a generic character which has not been sufficiently emphasized by writers. This is a peculiar enlargement at the apex of the branch, just below the perianth. It becomes evident after an archegonium has been fertilized, and is doubtless to be looked upon as one of

[27] Unters. über Lebermoose 2 : 10. 1875.

the secondary effects of fertilization. A longitudinal section through the female branch and young sporophyte of *O. Macounii* (*fig. 4*) shows this enlargement very clearly, and also shows how the bracts and perianth are inserted. The foot of the developing sporophyte together with a portion of the stalk penetrate into this enlargement, which is composed in large part of food-storing cells. The capsule and the remainder of the stalk are covered by the calyptra, at the base of which may be seen a few paraphyllia and unfertilized archegonia. In *O. Macounii* the enlargement is radial in structure, probably on account of the lateral attachment of the female branch. In such a species as *O. prostratum*, however, where the branches are very short and uniformly postical, the enlargement is not wholly symmetrical, but shows a slight bulging in the portion turned toward the substratum (*fig. 42*). In the related genus Adelocolea a very similar condition exists, and in certain species the bulging portion becomes more prominent and forms a bulbous base into which the foot of the erect young sporophyte forces its way. In the genus Marsupidium the extreme development of the enlargement is found in the form of a cylindrical perigynium, in which practically the whole of the sporophyte is imbedded.

It has already been noted that in *O. Macounii* the mouth of the perianth is wholly destitute of distinct teeth (*fig. 24*), and it may be added that these are not invariably present in other species. On *O. prostratum*, for example, much of the perianth-mouth is scarcely crenulate (*fig. 63*), and it is only occasionally that a short tooth, one or two cells long, can be demonstrated. Even in *O. Sphagni* and in *O. denudatum*, the teeth are often reduced to slight crenulations. The fact that the perianth is irregularly lobed at the mouth and often deeply plicate makes it difficult to gain an accurate idea of the true conditions. The difficulty is increased by the withering of the upper part of the perianth and by its irregular laceration when the mature capsule is extruded.

GEMMIPAROUS BRANCHES.

In distinguishing the different species of Odontoschisma, the gemmiparous branches often yield characters of importance. In

O. Sphagni and in *O. prostratum*, gemmae are apparently never produced, but they occur more or less frequently in our other species, and in *O. denudatum* they may be found even on fruiting individuals. In this species the gemmiparous branches are the upright continuations of prostrate branches, and the formation of the gemmae soon puts a stop to further elongation. The leaves and underleaves on these branches are scarcely distinguishable from each other; they are distant and strongly squarrose, and become smaller and smaller toward the apex of the branch. In *O. Gibbsiae* (*fig. 29*) and in *O. Macounii* the gemmiparous branches are prostrate or ascending, but they likewise show three ranks of leaves, the underleaves being distinguishable only by their position. In both these species the leaves are concave, loosely imbricated, and relatively longer than ordinary leaves. Sometimes a branch of this character attains a considerable length, but its growth is ultimately terminated by the formation of gemmae. In *O. Macounii* gemmiparous branches are much less frequent than in *O. Gibbsiae*. The gemmae themselves are similar in the different species. They are oval or spherical bodies and are composed of two cells, or more rarely of a single cell. In *O. denudatum* they are thin-walled, while in our other two species (*fig. 28*) they are thick-walled. In the lower part of a gemmiparous branch the leaves bear gemmae on their margins and outer surfaces; in the upper part the rudimentary leaves and the stem-apex become wholly transformed into a mass of gemmae.

COMPARISON OF THE GENERA ODONTOSCHISMA, ANOMOCLADA, AND CEPHALOZIA.

One of the most striking peculiarities of the genus Anomoclada, as described by Spruce, is the secretion by the underleaves of so much slime that it literally floods the entire plant. In the original paper on this genus[28] it was further stated that "the marginal and apical cells [of the underleaves] were continually swelling and discharging their protoplasm, adhering for awhile as empty bleached bladders, then falling away, for the succeeding cells to undergo the same process." Spruce also called attention to the

[28] Journal of Botany 5: 130. 1876.

difficulty of finding a perfect underleaf. An examination of the specimens of *A. mucosa* which were distributed in *Hepaticae Spruceanae* shows that the secretion of slime is performed by club-shaped papillae, similar in all respects to those described for Odontoschisma, and that it is not necessarily accompanied by the destruction of cells. The only difference between the genera in this respect is a difference of degree, the underleaves of Anomoclada being larger and the papillae more numerous than in Odontoschisma. They arise not only from the margin of an underleaf, but also from the postical surface near the margin, and sometimes a cell is directly transformed into a papilla. The basal cells of the underleaves acquire thickened walls with distinct trigones, and persist indefinitely, even after the papillae have lost their protoplasm and withered away. According to Spruce, the underleaves are "late ovata in acumen subulamve brevem producta . . . . superiora vix unquam perfecta, sed e margine apiceque plus minus dissolutis, nunc irregulariter bifida, nunc quadrifida vel digitatim multifida." As a matter of fact, the underleaves are variously divided, even in the vicinity of the growing point, and this division is in no sense due to the development of slime-secreting papillae. There seems to be no good reason, therefore, for considering that they are primarily undivided.

The strong resemblance between the underleaves of Odontoschisma and Anomoclada indicates a close relationship between the genera. They resemble each other further in their prostrate stems with postical flagella, in their succubous undivided leaves, and in their thick-walled leaf-cells with distinct trigones. Even closer to Anomoclada than any of the species which have yet been noted, is *Odontoschisma Portoricense*, a West Indian species (*figs. 65–74*). At first sight this looks precisely like a poorly developed form of *A. mucosa*, largely from the fact that its leaves are commonly crispate near the postical base and slightly convex—peculiarities which none of the more northern forms of the genus show. In *O. Portoricense* the underleaves (*fig. 70*) are covered over with slime-papillae, and the perichaetial bracts are often slightly connate (*fig. 71*), the latter being a character

emphasized for Anomoclada. The vegetative branches are occasionally lateral (*fig. 65*), but rarely recede very far from the postical base of the subtending leaf: so far as observed, the female branches are invariably postical. The only character of real importance which distinguishes Anomoclada from Odontoschisma is its antical branching. Whether this peculiarity by itself is sufficient to separate genera may well be questioned, especially when we take into account the great variability in the branching of Odontoschisma.

One of the connecting links between Odontoschisma and Cephalozia is *C. Francisci*, a rare species known from several localities in western Europe and recently detected in Maine.[29] It was, to a considerable extent, the existence of this species which influenced Spruce in including Odontoschisma among his subgenera of Cephalozia. *C. Francisci* is a true Cephalozia and has bifid leaves, but the lobes of the latter are commonly rounded or obtuse, instead of being sharp-pointed as is usual in the genus. Similar bifid leaves with rounded lobes are exceptionally found in *Odontoschisma Sphagni*, as Spruce has already noted, and they are not infrequent in *O. prostratum* (*fig. 43*). *C. Francisci* agrees with Odontoschisma further in its postical flagella, and in its irregularly bifid underleaves, the latter being built up on essentially the same plan as in *O. Sphagni* and bearing a very few secondary marginal papillae of short duration. The only characters which separate this species from Odontoschisma are its smaller size, its more delicate structure, and its regularly bifid leaves, not one of which can be regarded as of very great moment. In fact, the second of these differences is hardly worthy of mention, because the cell walls of *C. Francisci*, although thinner than is usual in Odontoschisma, are by no means wholly destitute of thickenings; these appear in the leaves as minute but distinct trigones, in the involucral leaves and perianths as more or less uniform thickenings tending to obliterate the trigones.

It will be seen, therefore, that although Odontoschisma represents a natural group of closely allied species, there is, on the one hand, a very vague line of demarcation between Odonto-

[29] *Cf.* Miss C. C. Haynes, Torreya 3:41. 1903.

schisma and Anomoclada, and, on the other hand, a similarly vague line between Odontoschisma and Cephalozia. In a certain sense our species of Odontoschisma form part of a continuous series, whose extremes are *Anomoclada mucosa* and *Cephalozia Francisci.* If we recognize three distinct genera in this series, it is largely because the two extremes are so very diverse. In the large group of the Lejeuneae we find these conditions duplicated, many of the recognized genera being connected by intermediate species.

DESCRIPTION OF SPECIES WITH NOTES ON GEOGRAPHICAL DISTRIBUTION.

Full descriptions of *O. Macounii*, *O. Gibbsiae*, and *O. prostratum* are appended. *O. Portoricense* is also described, although the present paper makes no pretense of revising the species of Odontoschisma found in the American tropics. For descriptions of *O. denudatum* and *O. Sphagni*, aside from the characters discussed in the preceding pages, reference may be made to the writings of Lindberg,[30] of Spruce,[31] and of Pearson.[32] For all five of our northern species the synonymy and geographical distribution are noted, and the following artificial key will aid in their identification:

1. Plants commonly growing on rotten logs or on banks, branches varying from postical to lateral, leaves more or less strongly concave, not margined, gemmiparous branches often abundant - - - - 2
1. Plants, commonly growing in bogs or swamps, branches always postical, leaves plane or slightly concave, more or less distinctly margined, gemmiparous branches wanting - - - - - - - - 4
2. Leaves and underleaves on the gemmiparous branches suberect, strongly concave and imbricated - - - - - - - - - - 3
2. Leaves and underleaves on the gemmiparous branches squarrose, plane or slightly concave and distant - - - - - 3. *O. denudatum*
3. Plants pale green or yellowish, leaves not dilated at the postical base, median leaf-cells averaging 28 μ in diameter, underleaves distinct and frequently conspicuous - - - - - - - 1. *O. Macounii*
3. Plants varying from pale green to reddish or brownish, leaves dilated at the postical base, median leaf-cells averaging 19 μ in diameter, underleaves usually minute and inconspicuous - - - 2. *O. Gibbsiae*

[30] Notis. ur Sällsk. pro F. et Fl. Fenn. Förhandl. 13: 357–360. 1874.

[31] Journal of Botany 5: 166, 193. 1876. On Cephalozia 60, 61. 1882.

[32] Hep. British Isles 171, 174. 1900.

4. Plants commonly brownish green, leaves broadly orbicular, usually erect and connivent antically, margin rarely more than one cell wide - - - - - - - - - 4. *O. Sphagni*
4. Plants pale green, more rarely tinged with brownish, leaves varying from oblong to orbicular but usually longer than broad, mostly explanate, margin from one to four cells wide - - - 5. *O. prostratum*

1. ODONTOSCHISMA MACOUNII (Aust.) Underw. Bull. Ill. State Lab. Nat. Hist. **2**: 92. 1884.—*Plate XVIII.*

Sphagnoecetis Macounii Aust. Bull. Torr. Bot. Club **3**: 13. 1872.

Sphagnoecetis communis, var. *tessellata* Berggr. Kongl. Sv. Vet. Akad. Handl. 13^7: 101. 1875.

Jungermannia tessellata Berggr. *l. c.* 13^8: 43. 1875.

Cephalozia (*Odontoschisma*) *Austini* Pears. List Canad. Hepat. 10. 1890.

Odontoschisma Sphagni, var. *tessellatum* Kaalaas, Vidensk. Skrift. I. 1898^9: 14.

Odontoschisma tessellatum C. Jensen, Meddel. om Grønland **15**: 369. *f. 1–4.* 1898.

Plants pale green or yellowish, rarely tinged with brown, growing in depressed mats or creeping among other bryophytes: stems sparingly and irregularly branched, 0.2^{mm} in diameter, prostrate, ascending at the tips; flagella postical, with very minute and rudimentary leaves; vegetative and sexual branches varying from postical to lateral, but usually occupying the latter position; rhizoids scanty, borne either on the flagella or on the postical surface of the stem and leafy branches, never on the underleaves: leaves imbricated, strongly concave, broadly orbicular, 0.75^{mm} long, 0.85^{mm} wide, not margined, attached by an oblique line of insertion, neither dilated at the postical base nor decurrent antically, margin entire, apex varying from broadly rounded to truncate or slightly retuse, very rarely indistinctly bilobed: leaf cells 25μ in diameter at the margin of leaf, 28μ in the middle and at the base, with very large, occasionally confluent and rounded trigones; cell cavities stellate with narrow pits; cuticle very thick, smooth: underleaves varying from minute to rather large, reaching a maximum length of about 0.2^{mm}, when well developed ovate to oblong in shape, rounded, retuse or irregularly bilobed at the apex, margin entire, but bearing numerous slime-papillae: inflorescence dioicous: ♀ inflorescence borne on a short branch; involucral leaves (bracts

and bracteoles practically indistinguishable) in three rows, leaves of innermost row slightly complicate, ovate, 1.4^{mm} long, 0.75^{mm} wide, bifid about one-fourth with narrow sharp-pointed lobes and sinus, margin subentire or bearing a few small and irregular lobe-like teeth, marginal papillae numerous, especially at the apices of the teeth; leaves of outermost row small and sub-orbicular, truncate at the apex or slightly bifid with a broad sinus, marginal papillae few, mostly at the base; leaves of middle row intermediate in character; perianth oblong in outline, contracted at the base and at the apex, 3.4^{mm} long, 0.95^{mm} wide, obtusely three-keeled, somewhat plicate in the upper part, mouth slightly and irregularly lobed, the divisions entire or very vaguely crenulate from projecting cells: ♂ inflorescence occupying a short branch; bracts in three or four pairs, complicate, slightly bifid or truncate, inflated near the antical base and commonly bearing a small inflexed tooth at about the middle of the antical margin; bracteoles similar to the underleaves; antheridia borne singly: capsule oval; spores brownish, minutely verruculose, 14μ in diameter; elaters 9μ in diameter, bispiral: gemmiparous branches long and worm-like, simple, terminating normal vegetative branches, prostrate or ascending; leaves in three equal ranks (the underleaves being similar to the side-leaves) sub-transversely inserted, imbricated, concave, oblong, variously erose-dentate along margin in upper part and at apex; gemmae oval to pyriform, arising singly or in chains from the margin and outer surface of the leaves and finally from the stem-apex, one-celled or usually two-celled, with a thick outer wall and a thin transverse partition, occasionally mixed with slime-papillae.

On banks. GREENLAND: Claushavn (*Berggren*); Cape Stewart (*Hartz*); Hurry Inlet, Cape Franklin, Cape Mary (*Dusén*). YUKON: Dawson (*Williams*); Hunker Creek, Gold Run Creek (*Macoun*). ONTARIO: "25 miles north of Michepicoten and near Otter Head, Lake Superior" (*Macoun*), the type localities. MINNESOTA: near Grand Marais, north shore of Lake Superior (*Holzinger*). Also reported from Spitzbergen (*Berggren*) and from Norway (*Kaalaas, Jörgensen*).

EXSIC.: *Can. Hep.* 101 (as *Cephalozia Austini*).

2. **Odontoschisma Gibbsiae**, sp. nov.—*Plate XIX, figs. 29–34.* Plants yellowish green, more or less tinged with red or brown, growing in depressed mats or creeping among other bryophytes: stems sparingly and irregularly branched, 0.3^{mm} in diameter, prostrate, ascending at the tips; flagella postical or terminating leafy branches; vegetative branches varying from postical to lateral; rhizoids scanty: leaves imbricated, strongly concave, increasing in size from the base of a leafy axis, orbicular, 1^{mm} long, not bordered, attached by an oblique line of insertion, slightly decurrent antically and more or less dilated at postical base, arching to or beyond the middle of the axis, margin entire, apex rounded: leaf-cells $16 \times 23\mu$ at edge, 19μ in diameter in the middle and 23μ at the base, with very large and occasionally confluent rounded trigones; cell cavities stellate with distinct pits; pigmentation when present limited to the lining of the cavity, not affecting the limiting membrane of the pits nor the outer part of the very thick smooth or minutely verruculose cuticle: underleaves minute, except at the base of a branch, irregular in shape, sometimes vaguely bidentate: inflorescence unknown: gemmae and gemmiparous branches similar to those of *O. Macounii* but the latter with more loosely imbricated leaves.

On a log. BRITISH COLUMBIA: Port Renfrew, Vancouver Island (*Miss Gertrude Gibbs*), the type locality.

3. ODONTOSCHISMA DENUDATUM (Mart.) Dumort. Recueil d'Obs. sur les Jung. 19. 1835.—*Plate XIX, figs. 35–38.*

Jungermannia scalaris, var. *β denudata* Martius, Fl. Crypt. Erlangensis 183. 1817.

Jungermannia denudata Nees; Martius, *op. cit. praef.* p. xiv. 1817.

Pleuroschisma (*Odontoschisma*) *denudatum* Dumortier Syll. Jung. Eur. 69. 1831.

Sphagnoecetis communis β macrior Nees, G. L. & N. Syn. Hep. 149. 1845.

Sphagnoecetis Huebneriana Rabenhorst, Deutschlands Krypt.-Flora **2**: 338. 1848.

Odontoschisma Huebnerianum Aust. Hep. Bor.-Amer. 61b. 1873.

Cephalozia (*Odontoschisma*) *denudata* Spruce, On Cephalozia 61. 1882.

Odontoschisma Sphagni β denudatum Massal. & Carest. Nuovo Gior. Bot. Ital. **14**: 238. 1882.

Odontoschisma Sphagni var. *macrior* Meylan, Bull. de l'Herb. Boissier II. **1**: 629. 1901.

On rotten logs, more rarely on shaded banks. GREENLAND: Scoresby Sound (*Hartz*). NOVA SCOTIA: Pirate's Cove and Baddeck (*Macoun*). NEW BRUNSWICK: Campobello (*Farlow*). ONTARIO: Ottawa and Bellville, (*Macoun*). NEW HAMPSHIRE: Shelburne (*Farlow*); Franconia (*Mrs. Curtis*); Jackson (*Evans*). VERMONT: Mt. Mansfield and Lake Dunmore (*Farlow*). MASSACHUSETTS: New Bedford (*Ingraham*); Magnolia (*Farlow*). CONNECTICUT: Windsor, Salisbury and Hamden (*Evans*). NEW YORK: near Syracuse (*Underwood*). NEW JERSEY: Delaware Water Gap and Bergen (*Austin*); Atsion (*Evans*). DELAWARE: Newark (*Commons*). DISTRICT OF COLUMBIA (*Holzinger*). VIRGINIA: Marion (*Mrs. Britton* and *Miss Vail*). NORTH CAROLINA: Salem (*Schweinitz*). OHIO (*Sullivant*). TENNESSEE (*Ruth*). FLORIDA: Monticello (*Lighthipe*). ALABAMA: Mobile (*Mohr*); Citronville (*Baker*). LOUISIANA: Covington (*Langlois*). Widely distributed in Europe and in northern Asia: also reported from tropical America.

EXSIC.: *Musci Alleg.* 229 (as *Jungermannia Sphagni*, var. 2); *Hep. Bor. Amer.* 61b (as *Odontoschisma Huebnerianum*); *Hep. Amer.* 124; *Can. Hep.* 102 (as *Cephalozia Sphagni*), 105 (as *Cephalozia deundata*).

4. ODONTOSCHISMA SPHAGNI (Dicks.) Dumort. Recueil d'Obs. sur les Jung. 19. 1835.—*Plate XIX, figs. 39–41.*

Jungermannia Sphagni Dicks. Fasc. Pl. Crypt. Brit. 1: 6. 1785.

Pleuroschisma (*Odontoschisma*) *Sphagni* Dumort. Syll. Jung. Eur. 68. 1831.

Sphagnoecetis communis α vegetior Nees, G. L. & N. Syn. Hep. 149. 1845.

Odontoschisma Sphagni var. *Europaea* Spruce, Journal of Botany 5: 167. 1876.

Cephalozia (*Odontoschisma*) *Sphagni*, Spruce, On Cephalozia 60. 1882.

Cephalozia Sphagni var. *Europaea* Spruce, Hepaticae Amaz. et And. 401. 1885.

In bogs, creeping over *Sphagnum* or *Leucobryum*. NOVA SCOTIA: Louisburg (*Macoun*). Widely distributed in northern Europe. The species has also been reported, in North America, from Greenland (*Berggren*), from Miquelon Island (*Delamare*), and from various localities in the United States, but all the latter references are probably incorrect.

5. ODONTOSCHISMA PROSTRATUM (Swartz) Trevis. Mem. R. Ist. Lomb. III. 4: 419. 1877.—*Plates XIX, XX, figs. 42–64.*

Jungermannia prostrata Swartz. Prodr. Fl. Ind. Occ. 142. 1788.

? *Sphagnoecetis prostrata* Nees; G. L. & N. Syn. Hep. 149. 1845.

Pleuroschisma prostratum Mitt., Challenger Rept. Bot. 1^2: 92. 1884.

Plants pale green, often tinged with brownish, growing in depressed mats or creeping among mosses and other bog-plants:

stems sparingly and irregularly branched, 0.25^{mm} in diameter, prostrate with ascending tips; branches all postical; rhizoids scanty: leaves distant to loosely imbricated, plane or slightly concave, varying in shape from orbicular to oblong, $0.7–1.4^{mm}$ long, $0.75–1.3^{mm}$ wide, distinctly margined, attached by an oblique line of insertion, slightly decurrent antically but not dilated at postical base, margin entire, apex commonly rounded, sometimes truncate, emarginate or bilobed: median and basal leaf-cells 20μ in diameter, thin-walled and with minute but distinct trigones; cell cavities polygonal with rounded angles; marginal cells $14 \times 23\mu$, forming one to four concentric rows and often arranged in radial rows as well, their walls more or less uniformly thickened with indistinct trigones; cuticle somewhat thickened, smooth or minutely verruculose: underleaves more or less persistent, linear to subulate in shape, 0.15^{mm} long, 0.05^{mm} wide, shortly bifid at the apex; slime papillae borne on the margin and more rarely on the postical surface, short-lived: inflorescence dioicous: ♀ inflorescence on a short branch; involucral leaves in about three rows, those of the innermost row 1^{mm} long, 0.5^{mm} wide, ovate, bifid about one-half with slender spreading acuminate lobes and narrow sinus, margin entire or with one or two slender lobe-like teeth below the middle; leaves of outermost row smaller and relatively broader, rounded or slightly bifid at the apex, margin entire; leaves of middle row intermediate in character; perianth linear-ovoid, 3^{mm} long, 0.9^{mm} wide, slightly contracted at the base and at the apex, obtusely three-keeled in lower part when young, terete when old, plicate in upper part, mouth irregularly lobed or cleft, the lobes subentire to short-setulose, the setae rarely more than one cell long: ♂ inflorescence occupying a short branch; bracts in about six pairs, complicate, shortly bifid with obtuse lobes and sinus, inflated near the antical base and commonly with a short and often inflexed tooth at about the middle of the antical margin; bracteoles larger than the ordinary underleaves, ovate, more or less distinctly bifid with subulate lobes; antheridia borne singly: capsule oval; spores brownish, 12μ in diameter, minutely verruculose; elaters 9μ in diameter, bispiral: gemmae wanting.

In bogs or swamps, more rarely on sandy banks or rocks. MASSACHUSETTS: Woods Hole (*Evans*). CONNECTICUT: New Haven (*Eaton*); North Branford (*Evans*). NEW YORK: Staten Island (*Underwood, Mrs. Britton, Howe*); Freeport, Long Island (*Howe*). NEW JERSEY: Delaware Water Gap and Closter (*Austin*); Locust and Highlands (*Miss Haynes*); Fort Lee (*Howe*); Avon (*Lloyd*); Atsion (*Evans*). DELAWARE: Wilmington and Newark (*Commons*). DISTRICT OF COLUMBIA (*Holzinger*). VIRGINIA: Nicks Creek, Marion, Dismal Swamp, and Virginia Beach (*Mrs. Britton* and *Miss Vail*). NORTH CAROLINA: Beaufort (*Johnson*). SOUTH CAROLINA: Summerville (*Miss Dubois*). GEORGIA: Tallulah Falls (*Underwood, Small*). FLORIDA: Amelia Island (*Eaton*); Grand Island, Lisbon, Eustis, and Blandton (*Underwood*); Port Orange and Lake City (*Straub*). ALABAMA: Mobile (*Mohr*). MISSISSIPPI: Bay St. Louis and Pass Christian (*Langlois*); Ocean Springs (*Seymour*). MISSOURI: Mine La Motte (*Russell*). ARKANSAS: Malvern (*Russell*). LOUISIANA: without definite locality (*Drummond*); Mandersville, Covington, St. Martinsville, and Opelousas (*Langlois*). Also reported from Jamaica (*Swartz*), the type-locality, from various other stations in tropical America and from Europe (see page 323).

EXSIC.: *Musc. Amer. St. Merid.* 161 (as *Jungermannia Sphagni*) *Musc. Alleg.* 228 (as *Jungermannia Sphagni*, var. 1); *Hep. Bor.-Amer.* 61 (as *Odontoschisma Sphagni*); *Hep. Amer.* 36 (also as *O. Sphagni*); C. Wright's *Hep. Cubenses*, without number (as *Sphagnoecetis prostrata*).

Very similar in appearance to *O. prostratum* are sterile specimens of *Jamesoniella autumnalis* (DC.) Steph. (=*Jungermannia Schraderi* Mart.), and the two species are often confused in herbaria, both being referred to *O. Sphagni*. *J. autumnalis* commonly grows on decayed logs, but is sometimes found on shaded banks or on rocks.. It has succubous undivided leaves and is of about the same size as *O. Sphagni*. It is, however, quite destitute of flagella; its leaves are not distinctly bordered, and its leaf-cells are slightly larger, averaging 21 μ in the middle of the leaf and 28 μ at the base. Of course, fruiting specimens of the *Jamesoniella* are very distinct, the perianth being terminal on a leading branch.

ODONTOSCHISMA PORTORICENSE (Hampe & Gottsche) Steph. Hedwigia, **27**: 296. 1888.—*Plate XX, figs. 65–74.*

Sphagnoecetis Portoricensis Hampe & Gottsche, Linnaea **25**: 343. 1852.

Plants yellowish green, growing in depressed mats: stems prostrate, sparingly and irregularly branched, 0.35^{mm} in diameter;

leafy branches varying in position from postical to lateral, flagella postical or terminating leafy branches, sexual branches (so far as known) postical; rhizoids scanty: leaves imbricated, plane or slightly convex, more or less crispate, oblong to ligulate, on robust stems reaching a length of 2^{mm} and a width of 1^{mm}, not margined, attached by an oblique line of insertion, slightly decurrent antically, more or less strongly dilated near the postical base, margin entire or irregularly sinuate, apex truncate or emarginate: leaf-cells averaging $23\,\mu$ in diameter at margin of leaf, $28\,\mu$ in the middle, and $32\,\mu$ at the base, with large, occasionally confluent, truncate or retuse trigones; cell cavities stellate with rather broad and truncate pits, cuticle thickened, smooth or minutely verruculose: underleaves minute, less than 0.1^{mm} long, ovate to broadly orbicular, apex commonly rounded; slime-papillae borne on the margin and on the postical surface, short-lived: inflorescence dioicous: ♀ inflorescence on a short branch; involucral leaves in about three pairs; leaves of innermost pair free or slightly connate at the base, ovate-oblong, 0.1^{mm} long, 0.4^{mm} wide, bifid about one-third with narrow acute spreading lobes and narrow sinus, margin entire or irregularly subcrenulate, sometimes with one or more lobe-like teeth at about the middle of the sides; remaining involucral leaves shorter and relatively broader, those of the outermost row orbicular, shortly bifid, with acute tooth-like lobes; perianth linear in outline, 3^{mm} long, 0.8^{mm} wide, slightly contracted at the base and apex, terete (when old) in lower part, plicate in upper part, mouth irregularly lobed or cleft, the divisions ciliate with cilia one to five cells long: remaining parts not seen.

PORTO RICO (*Schwanecke*), the type locality. CUBA (*Wright*).

EXSIC.: C. Wright's *Hep. Cubenses*, without number (under a manuscript name of Gottsche).

The type-specimen of *O. Portoricense* in the herbarium of the British Museum is a little less robust than some of the Cuban specimens distributed by Wright. It agrees, however, very closely with other specimens in Wright's collection, and the latter are connected by a series of intermediate forms with the

robust specimens. There seems to be no reason, therefore, for considering the Porto Rican and Cuban plants distinct.

There is no danger of confusing this very peculiar plant with any of our northern species of Odontoschisma. It differs from them, not only in its greater robustness, but also in its oblong to ligulate leaves with their edges parallel or nearly so except near the base. Other differences have already been indicated in discussing its relationship with *Anomoclada mucosa.*

In the preparation of this paper I have received valuable assistance not only from the botanists already mentioned but more especially from Professor L. M. Underwood, Professor W. G. Farlow, Dr. M. A. Howe, and Mr. W. R. Maxon. Through the kindness of these gentlemen I have been allowed access to the valuable herbaria under their charge and have also been provided with material for study from their private collections.

YALE UNIVERSITY.

EXPLANATION OF PLATES XVIII–XX.

The figures were drawn by the writer and prepared for reproduction by Miss Ednà L. Hyatt.

PLATE XVIII.

FIGS. 1–28. *Odontoschisma Macounii* (Aust.) Underw.

FIG. 1. Part of a plant bearing a lateral branch with perianth, antical view. × 20.

FIG. 2. Part of stem, postical view. × 20.

FIG. 3. Male inflorescence, antical view. × 45.

FIG. 4. Longitudinal section through female branch and young sporophyte, showing also the calyptra, two unfertilized archegonia, several slime-secreting hairs, the perianth and three perichaetial leaves; somewhat diagrammatic. × 45.

FIG. 5. Median leaf-cells, surface-view. × 400.

FIG. 6. The same, cross-section. × 280.

FIG. 7. Marginal leaf-cells. × 280.

FIGS. 8, 9. Young underleaves. × 280.

FIGS. 10–12. More mature underleaves. × 280.

FIG. 13. Cells from margin of a well developed underleaf. × 280.

FIGS. 14–16. Perichaetial bracts and bracteole, innermost row. × 20.

FIGS. 17–19. The same, second row. × 20.

FIGS. 20–22. The same, third row. × 20.

FIG. 23. Cells from middle of perianth. × 280.

FIG. 24. Cells from mouth of perianth. × 280.

FIGS. 25–27. Perigonial bracts. × 45.

FIG. 28. Gemmae. × 400.

Figs. 9, 11 and 12 were drawn from Minnesota specimens collected by Holzinger; the remaining figures were all drawn from the Yukon specimens collected by Macoun.

PLATE XIX.

FIGS. 29–34. *Odontoschisma Gibbsiae* Evans.

FIG. 29. Part of stem, gemmiparous and with three-ranked leaves above. × 18.

FIG. 30. Part of stem, postical view. × 18.

FIG. 31. Median leaf-cells. × 350.

FIG. 32. Marginal leaf-cells. × 250.

FIG. 33. Young underleaf. × 250.

FIG. 34. More mature underleaf. × 250.

The figures were all drawn from the type specimens.

FIGS. 35–38. *Odontoschisma denudatum* (Mart.) Dumort.

FIG. 35. Median leaf-cells. × 350.

FIG. 36. Marginal leaf-cells. × 250.

FIG. 37. Young underleaf. × 250.

FIG. 38. More mature underleaf. × 250.

The figures were drawn from Connecticut specimens collected by the writer.

FIGS. 39–41. *Odontoschisma Sphagni* (Dicks.) Dumort.

FIG. 39. Median leaf-cells. × 350.

FIG. 40. Marginal leaf-cells. × 350.

FIG. 41. Underleaf, antical view, not showing the slime-papillae on the postical surface. × 250.

The figures were drawn from specimens distributed in Gottsche and Rabenhorst's *Hep. Eur.* 399.

FIGS. 42–54. *Odontoschisma prostratum* (Swartz) Trevis.

FIG. 42. Part of a plant bearing a postical branch with perianth and a postical sterile branch. × 18.

FIG. 43. Part of stem, antical view. × 18.

FIG. 44. Part of stem, lateral view, showing flagella. × 18.

FIG. 45. Male inflorescence, antical view. × 40.

FIGS. 46–48. Perichaetial bracts and bracteole, innermost row. × 18.

FIGS. 49–51. The same, second row. × 18.

FIGS. 52–54. The same, third row. × 18.

PLATE XX.

FIGS. 55–64. *Odontoschisma prostratum* (Swartz) Trevis.

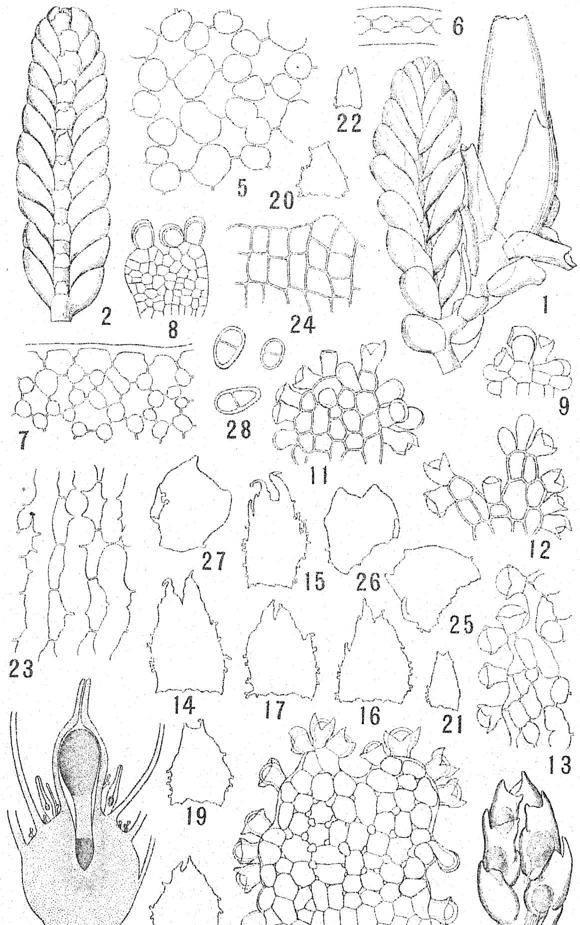
FIGS. 55, 56. Median leaf-cells. × 350.
FIGS. 57, 58. Marginal leaf-cells. × 250.
FIG. 59. Young underleaf. × 250.
FIGS. 60–62. More mature underleaves. × 250.
FIG. 63. Cells from mouth of perianth. × 250.
FIG. 64. Perigonial bracteole. × 250.

Figs. 56, 58, 61 and 62 were drawn from Cuban specimens distributed by Wright; the remaining figures were drawn from Connecticut specimens collected by the writer.

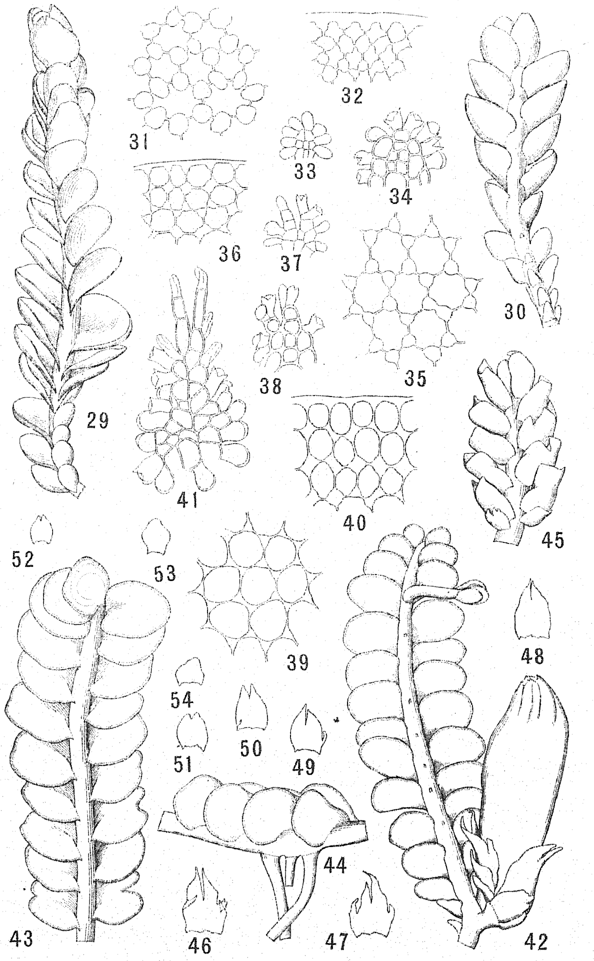
FIGS. 65–74. *Odontoschisma Portoricense* (Hampe & Gottsche) Steph.

FIG. 65. Part of stem with lateral branch, antical view. × 18.
FIG. 66. Part of stem, postical view. × 18.
FIG. 67. Female branch with perianth. × 18.
FIG. 68. Median leaf-cells. × 350.
FIG. 69. Marginal leaf-cells. × 250.
FIG. 70. Underleaf. × 250.
FIGS. 71, 72. Innermost bracts and bracteole from the same involucre. × 24.
FIG. 73. Innermost bract from another involucre. × 24.
FIG. 74. Cells from mouth of perianth. × 250.

The figures were all drawn from the specimens distributed in C. Wright's *Hepaticae Cubenses.*



EVANS on ODONTOSCHISMA.



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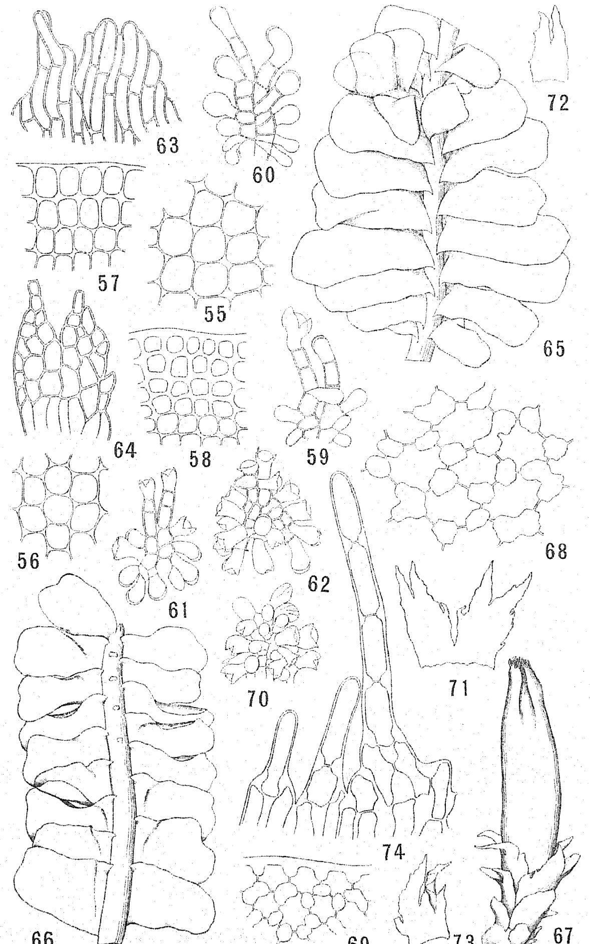

EVANS on ODONTOSCHISMA.

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

W. F. GANONG.

(*Continued from p. 302.*)

Synopsis of the grouping of the vegetation of the marshland.

A. HALOPHYTIC DIVISION, including the halophytic formations or HALOPHYTIA.

I. *Wild salt-marsh formation* (*Limnodium*).

1. Spartina stricta or *sedge* association, or SPARTINETUM.
2. Salicornia-Suaeda or *samphire* association, or SALICORNETUM.
3. Statice-Spartina juncea or *fox-grass* (*mezotte*) association, or STATICETUM.

B. MESOPHYTIC DIVISION (Culture section), including the mesophytic formations or MESOPHYTIA.

II. *Reclaimed salt-marsh formation = meadow formation* (*Poium*).

4. Phleum-Agropyrum or *timothy-couch* association, or PHLEUMETUM.
5. *Roadside weed* association, or CNICETUM.

C. HYDROPHYTIC DIVISION, including the hydrophytic formations or HYDROPHYTIA.

III. *Wet-marsh formation* (*Telmatium*).

6. Spartina cynosuroides or *broadleaf* association, or MACROSPARTINETUM.
7. Carex-Aspidium or *bog-marsh* association, or ASPIDETUM.

IV. *Bog formations.*

8. Carex-Menyanthes or *floating bog* association, or CARICETUM.
9. Heath or *flat-bog* association, or ERICETUM.
10. Sphagnum or *raised bog* association, or SPHAGNETUM.

V. *Water margin formation* (*Nematium*).

VI. *Swamp formation* (*Helorgadium*).

A. HALOPHYTIC DIVISION (HALOPHYTIA).

Consists of herbaceous plants of compact low growth, small size, and xerophytic structure, these features being determined by the presence of much salt, which both prevents the ready absorption of water requisite for large size and diffuse habit, and also, being itself injurious to the vital processes and not removable by plants from the absorbed water, requires the development of water-conserving adaptations to prevent its concentration in the tissues by transpiration. The division here includes but a single formation.

I. THE WILD SALT-MARSH FORMATION (LIMNODIUM).

Consists of slender-rooted and surface-following grass-like plants (this feature being determined by the fineness and compactness, and hence the poor aëration of the soil, which does not permit thick roots), mostly wind- or self-pollinated and wind-disseminated and late blossoming. The area of the salt-marsh has been restricted to a small fraction of the original area by reclamation through diking, and includes at present only a fringe outside the dikes,[36] together with certain points (shown in *fig. 2*) unprofitable from their form to dike. The formation here includes three associations.

I. THE SPARTINA STRICTA, OR "SEDGE" ASSOCIATION, OR SPARTINETUM.

The characteristic association of the immediate edge of the salt water extending typically as a belt just above and below ordinary high-tide mark and further distinguished to the eye by its bright green color, and the stiff habit and close growth of its plants (*figs. 7, 8, 9, 10, 11*). It extends also in isolated clumps much below high-water mark (the "sedge-bogs"), follows the ditches inside the dikes, occupies depressed areas amongst the Staticetum on high marsh, and takes possession of the lakes in process of reclamation. The association comprises but a single vegetation-form as follows:[37]

[36] This fringe extends not only along the sea but also along the rivers to near their heads (as shown by *fig. 7*), though for the sake of clearness this is not shown on the map, *fig. 2*.

[37] There occurs sometimes with it, or at all events in its situation, and especially on the little "cliffs" where the high marsh is being worn away, an abundance of a green alga, *Enteromorpha clathrata* (Roth.) J. Ag. (auc. G. T. Moore).

SPARTINA STRICTA GLABRA Gray. *Spartina stricta maritima* (Walt.) Scribn. *Figs. 9–10.*—Called in the marsh country *sedge* (usually pronounced "sage"). The most characteristic and extreme

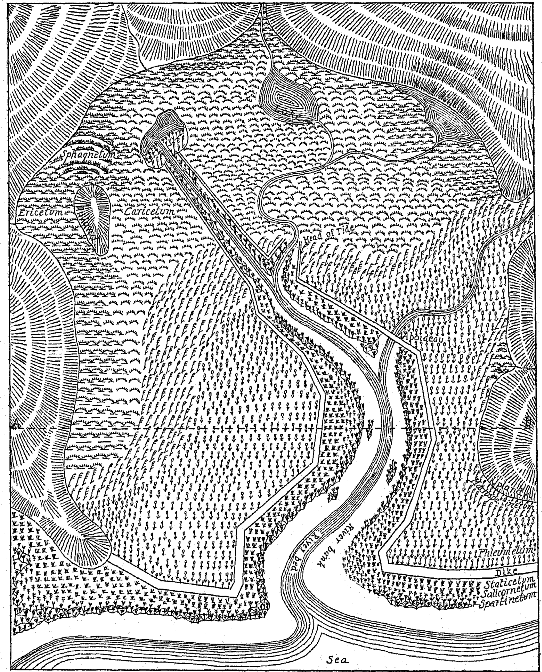

FIG. 7.—Diagrammatic map of a typical portion of the marshland, showing the ideal distribution of the principal associations (excepting the Aspidetum, on which see *infra*). In the upper left hand is a lake in process of reclamation; on the river banks are represented three of the "sedge-bogs." The line *AB* is the position of the cross-section shown in *fig. 8*.

salt-enduring plant (halophyte) of the marshes, following everywhere except on the newest marsh the margin of the salt water, from the open sea, where it is stunted to 6 in (15 cm) or less in height, along the tidal rivers, where it forms on their sloping banks much below high-tide mark dense clumps of a few square feet in area (locally called "sedge-bogs"), following the salt water through leaky sluices inside the dikes, and elsewhere in ditches behind the dikes, and reaching its perfection of size, some 3 to 4 ft (1 to 1.30 m) in the brackish water of the lakes in process of filling with new mud. It is the dominant and the only member of the association (Spartinetum) in which it occurs.

This species is a very typical representative of an important

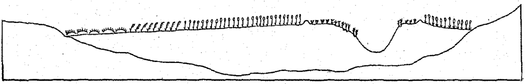

FIG. 8.—Cross-section of the region represented in *fig.* 7, at the dotted line.

vegetation-form. It consists of a system of perennial branching rootstocks running just beneath the surface, well sheathed by leaf bases, giving off extremely slender roots, protected by a fine-celled, thick epidermis and containing numerous large air passages, which, in connection with those of the leaves, explain the plant's power to withstand prolonged immersion. From the rootstocks rise frequent short vertical stems, completely and tightly enwrapped and protected by the bases of the half dozen or more stiffly erect, more or less inrolled slender leaves, their sizes varying inversely with the degree of salt to which they are exposed. The leaves are smooth on the back, which is covered by a very small-celled, thickly cutinized epidermis supported by a collenchymatous and sclerenchymatous hypodermis, and is probably quite impenetrable to water and gases; their inner face, however, is folded into deep grooves, at the bottoms of which lie few stomata, with the large water-storing cells near them. The mechanism appears to be such that the fulness of the latter cells holds the leaf flat, thus opening the grooves, giving the stomata free outlet to the atmosphere outside, but the withdrawal of

some of this water allows the elastic back to curl the leaf and close up more or less the grooves and hence protect the stomata, one of the most efficient regulatory mechanisms to control transpiration according to water supply known to me. Chlorenchyma is palisaded especially towards the inner face; large air spaces exist, communicating with those of the root, and the epidermis is not wetted by water, all permitting the immersion of the plants

FIG. 9.—Showing the three typical associations of the salt marsh. The Spartinetum on the left and the Staticetum (with its marginal Statice) on the right are advancing upon the Salicornetum in the center.

for some time. It propagates apparently mostly by rootstocks, and good seeds and seedlings appear to be rare. It is wind-pollinated and wind-disseminated.

Its specific physiological correlations appear to be unstudied. On account of the failure of all my seeds to germinate, I was unable to determine the resistance of its root-hairs to plasmolysis, but analogy with Salicornia would lead us to expect a high degree of resistance.[38]

[38] It seemed to me likely that the power of the halophytes to stand salt might be connected with a power in their root-hairs to withstand plasmolysis by sea water. Accordingly I procured some pure sea-water from Baie Verte, N. B., and, with distilled

The ability of this form to occupy its peculiarly trying habitat, with its abundant salt, frequent and prolonged immersion, and shifting substratum are amply explained by its adaptive structures above considered, notably its xerophytic anatomy combined with a very perfect transpiration-regulating mechanism, its capacity for copious air storage, and its system of interlacing, firmly anchored rootstocks, to which may be added the probable specific power of its root-hairs to resist plasmolysis by salt water. It is of course because no other plant possesses anywhere near the same combination of qualities that it reigns supreme, without competitor or companion, in its own peculiar habitat. There are forms which can stand as much immersion, and forms which can stand as much salt, but no forms which can stand a combination of these two conditions in so extreme a degree.

Like all other associations it tends to spread outside its own typical habitat. With the slow, irresistible, phalanx-like advance of its rootstocks, it easily enters the habitat of the Salicornetum, and utterly defeats and destroys that association ; it then advances upon the Staticetum against the margin of which it can prevail, to some extent, but ultimately it is overcome by that association, excepting where depressions with their salter soil enable colonies of it to thrive. In the lakes it is finally overcome by the broadleaf.

water, made solutions of all strengths from 10% to 90%. I gathered all the seeds of halophytes I could procure myself or by aid of a correspondent at Sackville (Mr. F. A. Dixon), and started them with fresh water in Zurich germinators. As soon as root-hairs appeared I tested them with the various solutions, and noted for each kind the solution which just initiated plasmolysis. I found a close correspondence between the halophilism of the plant and the power of its root-hairs to resist plasmolysis, the details being given with the various species in the following pages. This shows that the power of the plants to resist the salt water is correlated with and probably dependent upon the ability of the root-hairs to resist plasmolysis. This power has of course been gradually acquired, but what its physical basis is I do not know; though we shall probably find that substances osmotically equivalent to the salt of the sea-water have been formed in the sap of the hairs. In several cases (Hordeum, Couch) it was noticeable that no plasmolysis occurred with certain solutions as long as the hairs were alive, but it occurred after they were dead. Several forms (Statice, Plantago) showed marked jelly-like caps to the young roots, seemingly an adaptation to slower water-entrance. The study of the roots of these halophytes will give interesting results.

2. THE SALICORNIA-SUAEDA OR SAMPHIRE (LOCALLY CROWFOOT) ASSOCIATION, OR SALICORNETUM.

The characteristic association of the newly formed and forming marsh, occurring typically from the lowest high-tide marks to the highest marsh, hence overlapping the territory later occupied by the Spartinetum from below and the Staticetum from above, and further distinguished by its usually loosely open

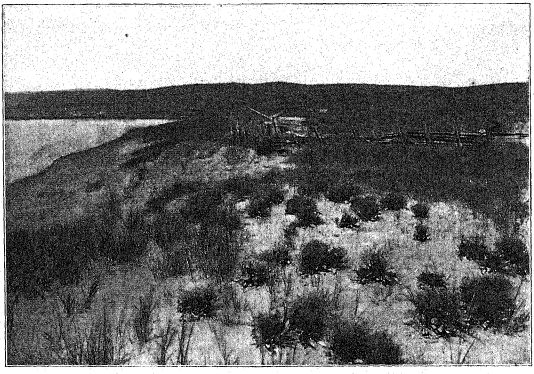

FIG. 10.—Showing Spartinetum on the left (and occupying a depression on the right) advancing upon the Staticetum (showing Statice clearly) in the center. Salicornetum obliterated between them as an association, but occurring as scattered individuals in the other associations. The fence-like structure is a protection to the dikes against the wash of the sea.

formation, the small size and succulent habit of its members, and their usually reddish color (*figs. 7, 8, 9, 12*). It extends inside the dikes, especially on newly flooded marsh, along the marsh roads and on the bald places, and upon any newly exposed marsh soil, as on new dikes, ditch margins, dredge-mud, etc. It is especially well developed where cattle run on the salt marsh, apparently because the cattle keep down the Spartinetum and Staticetum. In general its members are smaller, more stiffly upright, sparser, and redder the salter the place, and are more

luxuriant, larger, more spreading, and greener the fresher the place.

The association is composed of two dominant members, *Salicornia herbacea*, or samphire, and *Suaeda linearis*, which appear to be as a rule about equally abundant and prominent, and of two secondary forms, especially coming in on the higher and drier side, *Spergularia borealis* and *Atriplex hastatum patulum*.

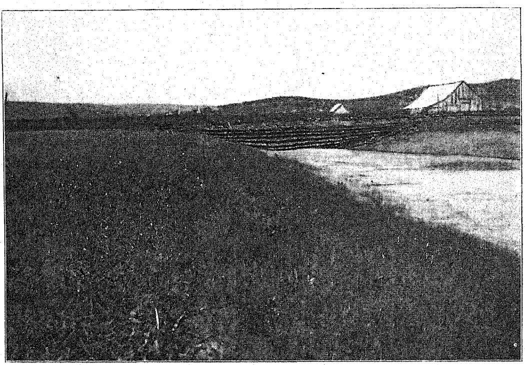

FIG. 11.—Showing Spartinetum on the river bank on the right advancing on the Staticetum on the left, with contact line in the center. The Statice can be seen within the margin of the Spartinetum. In the background is an aboideau crossed by a railroad.

SALICORNIA HERBACEA L.—Called in the marsh country crowfoot, and sometimes samphire. Next to the Spartina the most abundant and characteristic halophyte of the marshes, mixing occasionally with the Spartina, but commonly in a belt landward of it and hence in less wet situations; especially characteristic of the zone between the high-tide marks of neap and spring tides, and of newly forming marsh on convex river curves, where it is often the only plant for considerable areas, but being an annual it is somewhat irregular in distribution (*figs. 9–12*). In the saltest

places it is not over three inches (8^{cm}) in height, red in color, and stiffly erect; extends also inside the dikes on the bald places and along the roads, where it may become several times larger, decumbent and spreading and clear green. The dominant member of the Salicornetum.

Its vegetation-form is well-known and characteristic. It is a fibrous rooted annual, with a jointed, branching, succulent, prac-

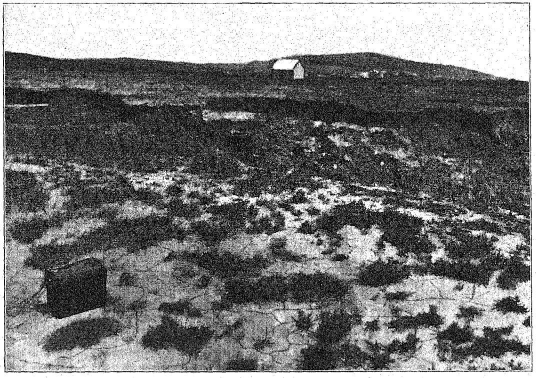

FIG. 12.—Showing a typical piece of Salicornetum on new marsh.

tically leafless stem, tending to verticality of green tissues, varying in size inversely with the saltness of the habitat. Its anatomy is markedly xerophytic, for in addition to the reduction of surface, the jointing and verticality described above, it possesses a compact stele (with cortical system of bundles replacing those of the abandoned leaves) thick water-storing cortex, dense palisaded chlorenchyma, small-celled thick-cuticled epidermis, small and narrow-slitted stomata, all markedly xerophytic features. The air storage system, however, is limited, consisting of intercellular spaces of ordinary size, and certain air-storing tracheids near the stomata. This is sufficient, however, to per-

mit the occasional immersion which the plant undergoes at the higher tides, but is insufficient to permit immersion so prolonged as that of Spartina. It is this feature that determines the difference in position of the two plants; the Salicornia can apparently stand as much salt as the Spartina, but it cannot stand long immersion, and hence it is confined to a higher position on the river banks.[39]

The physiological correlations of the species appear not to have been studied. I have, however, found that the root-hairs of the seedlings can withstand without plasmolysis a solution of 90 per cent. pure sea-water, which fact helps to explain its halophytic capacity. It is wind-pollinated, and apparently, wind-disseminated, though the seeds are provided with hooked hairs. It appears to me to be polyembryonic.

SUAEDA MARITIMA Dumort. *Dondia maritima* (L.) Druce.—Appears to have no local name. Occurs most commonly intermixed with the Salicornia, though extending into less salt places, and forming the second member of the Salicornetum (*fig. 12*).

Vegetation-form in a general way approaching that of Salicornia, but a leaf- instead of a stem-succulent and much less markedly xerophytic. Its root-hairs can endure 60–70 per cent. salt water without plasmolysis. Fibrous-rooted annual with semi-succulent stem, usually prostrate but sometimes in saltless places erect, with efficient epidermis having a thick cuticle and much collenchyma, bearing numerous somewhat succulent bluish green slender leaves which can be up to 2^{in} (5^{cm}) long. Leaves with large rounded epidermal cells, and stomata about equal on all faces, dense palisaded chlorenchyma and some water-storing cells. The leaves afford some protection against transpiration to one another and the stem by overlapping. Little trace of air-storing system, and hence not enduring immersion well, which explains why it grows rather higher on the beaches than the Salicornia. It is wind-pollinated and apparently wind-disseminated.

SPERGULARIA BOREALIS Robinson. *Tissa Canadensis* (Pers.)

[39] Diehl's conclusions that this plant has a power of removing salt chemically from its tissues are not substantiated.

Britton.—Apparently has no local name in the marsh country. Occurs to some extent with the Suaeda and Salicornia but belonging to less salt and wet places than either, and hence characteristic of the very highest and driest spots of the wild marsh; especially prone to wander inside the dikes on low places and along the roads.

Vegetation-form nearly identical with that of Suaeda, but smaller, more profusely branched and decumbent, and more leafy, with the leaves somewhat more slender. It is of a brighter green than the preceding, and unlike any of the preceding, bears pale pink or whitish star-like apparently entomophilous flowers.

ATRIPLEX PATULUM L., vars. *hastatum* Gray and *littorale* Gray. *Atriplex patula* L. and *A. hastata* L.—Appears to have no recognized local name. Occurs with the Salicornia and Suaeda, especially on their drier side, when it is not much taller than they, as a rather inconspicuous member of the Salicornetum, but extends also upon the dikes, when it occurs as a band, usually on the inner, lower side of the dikes; extends also within the dikes, especially upon newly flooded marsh, where it may become waist high.

The species represents a distinct vegetation form, a fibrous-rooted annual with erect stem and petioled hastate (var. *hastatum*) or linear (var. *littorale*) leaves, the whole plant varying in size from a few inches on the saltest places to near 3^{ft} (1^{m}) on newly flooded marsh. The plant exhibits in its vertically adjustable leaves which are extremely well marked in the young state on the salt marsh, in its thick cuticle, dense palisade, and its abundant covering of scales (giving it its characteristic scurfy or mealy appearance), xerophytic adaptations, adapting it to its halophytic habit. Its root-hairs endure nearly 40 per cent. salt water without plasmolysis. There appears to be no constant relation between the distribution of the linear and the hastate leaved forms and the environment, though each kind occurs as a rule largely by itself. It is wind-pollinated and wind-disseminated.

The chief characteristics of this association as a whole, its rapidity of appearance on new marsh and its ability to endure

much salt but little immersion, are amply explained by the adaptations of the members above described, notably their annual character and excellent mode of dissemination, their xerophytic structure, and the power of salt resistance possessed by their roots (at least in the two dominant members).

The members of the association grow often fairly intermingled, but elsewhere one or the other form may predominate, even for a considerable area, to the exclusion of the others. This irregularity of commingling is probably due to the fact that, all of them being annuals, the precise place of their occurrence in any given year is largely a matter of accident, due to the way the seed distributing agencies of wind and water happened to drift them the preceding year. Another irregularity comes from the general tendency for the Salicornia to be nearest the water, the Suaeda next, the Spergularia and Atriplex last, a distribution amply explained by the comparative degrees of xerophilism and air-storing capacity of the members, as above described.

Since the members are all annuals, all of nearly the same size, and all grow in an open order interfering little with one another, it is possible that this association is simply a mixture of forms which happen to be adapted to a similar habitat, with no ecological bond, but only coincident interests, between the members. Indeed, in the present state of knowledge, it is impossible to say that this is not the case with the members of all associations, though I think not, as will later be discussed.

Although thus very prompt to take possession of new marsh, this association can hold its ground only temporarily, for the slow-moving Spartinetum advances upon it from below, and the Staticetum upon it from above, until between the two it vanishes, and disappears as an association from old marsh, existing only as scattered individuals, visitors, among the other associations. It represents a sort of annual light infantry quick to occupy new territory, but easily displaced by the resistless advance of the heavy phalanxes of the perennial associations.

The readiness with which this association takes possession of new marsh makes it the first to appear on the new surface produced by artificial flooding. When the tide is shut out all the

members increase immensely in size, even, in the case of Atriplex, to waist high, after which they are displaced by the perennials. But this subject will be considered later under another heading.

3. THE STATICE-SPARTINA JUNCEA, OR FOX-GRASS (LOCALLY MEZOTTE) ASSOCIATION, OR STATICETUM.[40]

The characteristic association of the highest salt marsh, overflowed only by exceptionally high tides, and representing the highest development of salt-marsh vegetation—its matured condition (*figs. 7, 8, 9, 10, 11, 13, 14*). Distributed on all the

FIG. 13.—Typical piece of mature Staticetum showing Hordeum (barley-grass,) prominent in the center, and some scattered *Spartina cynosuroides* (broadleaf), etc. The finer grass is the *Spartina juncea* (fox-grass), and with it is some Statice.

highest parts of the wild salt marsh, and occupying the berme-bank built by the sea along the rivers outside of the dikes, and distinguished by its dull-green color in various shades, and the very dense, almost turf-like growth of its grass-like plants. It forms real salt meadow (yielding the salt-marsh hay), but is little luxuriant as compared with the meadows of the reclaimed marsh. It does not often, if at all, extend as a whole within the dikes, although some of its members do. Its dense growth appears to enable it to stop some of the mud brought to it by the very high-

[40] Statice is not so characteristic of this formation as is *Spartina juncea*, and it would be better called *Spartinetum* were that name not preempted for the Spartina stricta association, which latter having but a single member, of course admits of no other name.

est tides, by which, with the aid of its own decaying parts, it can build itself somewhat above the marsh, thus affording conditions for a limited mesophytic herbaceous vegetation, though this appears never to go very far, and never to include any woody plants whatsoever. In other places, small abrupt knolls of similar vegetation occur, which appear to be due to low hillocks pushed up by floating ice, though this point is uncertain. This association is composed of two dominant, with several secondary and some occasional members, as follows:

STATICE LIMONIUM CAROLINIANUM Gray. *Limonium Carolinianum* (Walt.) Britton.—Locally called wild cabbage. A very characteristic plant of the marshes, an important member of the dense vegetation of the high marsh with which it is much intermixed, and beyond which it extends in scattered clumps on new marsh, thus forming the vanguard in the advance downward upon the Salicornetum; also frequently in a band along the lower outer side of the dikes (*figs. 10, 11*).

A very marked vegetation-form, and the only one of the kind on the marsh; a rosette perennial, producing a cluster of radical petioled broad smooth leaves, usually so numerous as to afford one another much protection, and capable of much change of position according to surroundings. The plants are smallest on the saltest places, with leaves but $2–3^{in}$ ($5–8^{cm}$) long, and largest on the high grassy marsh when the leaves may be nearly 12^{in} (30^{cm}) long. Its leaves, stem, and root all possess a very abundant mucilage (apparently its chief xerophytic character), occurring even in the epidermis, and apparently intermixed with much tannin (which turns the plant black in formalin), a well but not extremely developed epidermis and cork. Its root-hairs can endure 50 to 60 per cent. of salt water without plasmolysis. It appears to attain its full size in a single season from seed, which explains the rapidity with which it takes possession of new marsh. It blossoms very late (in full bloom August 27, 1899), like other halophytes. Insect- and wind-pollinated. Like some other halophytes, it forms a jelly coating around its young roots, especially at the cap.

PLANTAGO MARITIMA L.—Locally called goose tongue. Occurs

abundantly among the Statice, especially as the latter advances on new marsh and at times in areas by itself; also sparingly with the *Spartina juncea*, as a fairly constant but not prominent member of the Staticetum.

A distinct vegetation-form, a stemless perennial with radical cluster of a few succulent linear leaves, giving it a somewhat grass-like habit. Its structure is moderately xerophytic, with thick cuticle and densely palisaded chlorenchyma. Wind-pollinated and wind-disseminated. Its size varies from 3 or 4^{in} (7–10^{cm}) high in the saltest places to 12^{in} (30^{cm}) in less salt places. It forms a jelly coating over its root cap, and can withstand nearly 60 per cent. of salt water without plasmolysis.

SPARTINA JUNCEA Willd. *Spartina patens* (Ait.) Muhl.—Fox grass or mezotte.[41] The most abundant and characteristic grass of the high salt marsh, intermingled with the other plants in the Staticetum, and also occurring in dense mats, especially in the slight depressions next the dikes. Rarely cut for hay. (*Figs. 13, 14.*)

A representative vegetation grass-form, composed of slender branching rootstocks, sending down very slender roots, and sending up very copious culms 6–12^{in} (15–30^{cm}) in height, bearing slender inrolled leaves of somewhat xerophytic structure.

PUCCINELLIA MARITIMA Parl.—Occurs amongst the Statice in isolated bunches, and also in larger isolated patches amongst the *Spartina juncea*. Distinguished from the Spartina by its larger size, lighter color, and tendency to grow in radiating tufts.

A vegetation-form not very different from the *Spartina juncea* but tending to grow somewhat after the manner of a bunch grass, especially as it appears on new marsh.

FESTUCA OVINA L.[42]—Occurs intermingled with *Spartina juncea* and Puccinellia, and very like them in vegetation type.

JUNCUS GERARDI Loisel.—Black grass. Occurs in dense radi-

[41] So pronounced locally; it is an Acadian French word, used (as misette) in 1685 or earlier (Casgrain, Un pèlerinage au pays d'Évangéline—29. Paris, 1890.).

[42] When the Puccinellia and Festuca grow together densely, as they sometimes do on the marsh, it is not easy to distinguish them unless in blossom, and I may be somewhat in error as to their relative abundance and part in the association. It is possible, too, that some others may occur which for this reason I have missed.

ating clumps in the Staticetum, but not especially abundant. Vegetation-form approaching closely to the grasses amongst which it grows.

TRIGLOCHIN MARITIMA L.—Scattered irregularly and not abundantly in the Staticetum, but more abundantly on the wet fresh marsh. Vegetation-form closely approaching the grasses amongst which it grows.

HORDEUM JUBATUM L.—Barley grass. Occurs upon the highest

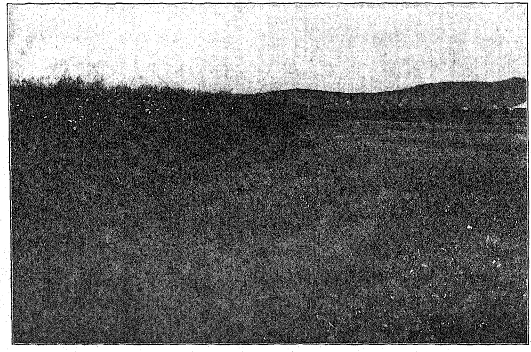

FIG. 14.—Showing a dike with Agropyrum (Couch) on the left, and typical Staticetum on the right. Beside the dike, in the center, is a zone of pure *Spartina juncea* (fox-grass).

part of the salt marsh (*fig. 13*), where it often is in great abundance and very conspicuous; also on the dikes in places, and especially abundant upon newly flooded marsh.

Vegetation-form near to other grasses, but with an unusually perfect system of dissemination, and apparently able to grow as an annual, whence the rapidity with which it enters new places. Its root-hairs stand over 40 per cent. pure salt water without plasmolysis.

GLAUX MARITIMA L.— Occurs scattered among the other members of the Staticetum, and apparently little gregarious.

A perennial herb of somewhat fleshy structure, not occurring in as salt places as its appearance would imply.

All of the members of this association are characterized by a moderately xerophytic structure, but with little provision for air storage, explaining well their position as occupants of the high marsh, which is rarely overflowed and from which a part of the salt at least is removed by superficial drainage.

The dominant members of the association are the Spartina (fox-grass or mezotte) and the Statice, with the Puccinellia and Plantago as important secondary members, and Festuca, Juncus, Triglochin, and Hordeum as less important, while Glaux is subordinate. The Spartina is the most important of all, forming the greater part of the association on the high marsh, and occurring here and there, especially in the slight depressions just outside the dikes (*fig. 14*), in large stretches unmixed with the others. In such places it forms a dense close turf. Elsewhere the Statice occurs intermingled with it (*figs. 9, 13, 14*), probably in such positions deriving some protection from transpiration for its broad leaves by the shade of the Spartina, but the Statice is especially important as the marginal member of the association particularly in its advance upon new marsh (*figs. 9, 10, 11*). It advances upon and displaces the Salicornetum, and then engages the Spartinetum advancing up the beach, the two associations mingling along the line to some extent (*figs. 10, 11*). The line of contact between these two represents one of the lines of competition to which I have given much study, with no results of value. When advancing in this way upon new marsh the Statice often forms so distinct a band that one is tempted to assign it to an association by itself, the more especially as it also so often occurs in a band on the angle of the dikes just inside of the fox-grass (*fig. 15*); but the luxuriance with which it grows along with the fox-grass shows it to be properly a member of the same association with that, while its distinctness on new marsh is plainly due simply to its more rapid power of spread. Closely following and intermingling with the Statice comes the Plantago, which also sometimes exhibits an indistinct band by itself, particularly between fox-grass and Statice. Intermingled with the

fox-grass comes the Puccinellia, which occurs in scattered dense radiating clumps, like a bunch-grass, in part here and there amongst the fox-grass, from which it is distinguished by its lighter color, and in part as scattered clumps on new marsh following the Statice in its advance. The Festuca is less common but grows somewhat after the same manner, as indeed does the Juncus or black grass. Triglochin occurs scattered among the other members, and seems equally at home here and in the fresh-water associations later to be noted, and Glaux is likewise scattered. Hordeum comes in only when the association reaches its greatest development on the highest marsh, and it occurs often as a band on the dikes above the other members. Scattered plants of Spartina stricta, Salicornia, Suaeda and Atriplex also occur as visitors, especially with the Statice. When this association reaches its greatest development on the highest marsh, it consists of a dense closed growth of all of the forms intermingled, and this constitutes the characteristic mature marsh. Upon it then develops the Hordeum (*fig. 13*). In this condition it can apparently build itself somewhat above the general marsh level, in part through the aid of the mud held by the plants when brought to them by the occasional extreme tides, and in part from the decay of their own members; and upon the higher places of this kind come in the occasional visitors, the broadleaf (*Spartina cynosuroides*), the couch (*Agropyrum vulgare*), *Potentilla anserina*, goldenrods, and others. But these represent the highest development; so far as any parts of the marshes now show, no woody vegetation ever gains a foothold.

It is plain that within this association while the members occur variously intermingled, there is some differentiation of position. Thus, typically the marginal member is the Statice, which is followed by the Plantago and the Puccinellia, while the fox-grass comes next, then the Festuca, Juncus, Triglochin, Glaux, and finally the Hordeum. Further, the marginal members tend to some extent to lessen, or even disappear towards the central or higher parts. This tendency to a zonal arrangement shows itself with great clearness upon the outer faces of the dikes, where there is usually a band of Statice at the lower angle,

then above it comes often a band of the Hordeum, above which comes the couch, later to be noticed.

The true ecological relationships of the several forms to one another, to what extent they are brought together simply by coincident habitat, to what extent they are of mutual benefit or disadvantage, to what extent some profit by the presence of others and those others are indifferent to them, to what extent and by what method they compete with one another, is unknown, and must be determined by the studies of the future. Such hints as we have upon these matters are little better than guesses, and such they will remain until thorough experimental study shall give the answer to these most difficult problems.

The interrelations of the three associations within the salt marsh formation have been sufficiently indicated in the preceding pages. In summary, the Spartinetum is the association of the extreme position where higher plant life is possible; the Salicornetum is the temporary association of new marsh; the Staticetum is the permanent association of the salt marsh in its highest natural state of development. On old marsh, the Spartinetum and Staticetum come together, obliterating the Salicornetum. The adaptations determining this distribution are known to us in a general way, but in details hardly at all.

(*To be concluded.*)

AN ECOLOGIC STUDY OF THE FLORA OF MOUNTAINOUS NORTH CAROLINA.

JOHN W. HARSHBERGER.

(*Concluded from p. 258.*)

THE VEGETATION OF THE MOUNTAIN REGION.

THE characteristic features of the vegetation of this whole region are found in the broad-leaved species, of which it is largely composed, associated with deciduous and evergreen shrubs, while lianes stretch from tree to tree, and herbaceous plants grow beneath the dominant forest species, or clothe the natural meadows of the higher mountain summits and the alluvial bottoms of the principal mountain streams. The association of these plants in the forest is largely due to their relation to light, soil, and moisture.

Relation to light.—All trees require a certain intensity of light for photosynthesis. Hence weak light is injurious; otherwise there is no reason why the foliage in the interior of the crowns of the trees should not be as dense as near the periphery. Marked differences occur among the various species of trees with regard to the measure of light necessary, and though affected by soil and situation, these differences are sufficient to admit of classification into tolerant and intolerant species; that is, into shade-bearing or light-demanding trees, and trees that occupy an intermediate position.[25] The different trees of the forests of North Carolina may be classified accordingly, as to their tolerance:

Sugar maple, flowering dogwood.
Hornbeam.
Red maple, yellow oak, beech.
Butternut, black walnut.
Witch hazel, chestnut oak, white oak.

[25] NISBET, Studies in forestry 54. 1894. FOLEY, JOHN, Conservative lumbering at Sewanee, Tennessee. Bureau of Forestry, Bull. 39.

White ash, umbrella tree.
Sweet gum, sycamore.
Locust, black cherry, sassafras.
Cucumber tree, chestnut.
Tulip tree.

The vegetation of such a district, therefore, is in superposed layers or stories. The different levels at which plants grow is a direct response to the environmental conditions of light and moisture. These stories or layers may be termed vegetal strata. It is evident that, as one ascends from the ground to the crown of the dominant forest trees, the moisture content of the air decreases as the light increases. On the ground in the forest, mosses, ferns, and a variety of shade-loving herbaceous plants abound on the rotting timber, or on the mold.

A relationship exists between the amount of available light and the character of the vegetation in the forest.[26] Almost all of the plants growing in the shade can adapt themselves to living in the open, exposed to the full force of the sunlight. In fact, when the timber is removed, the grass-grown or wood-grown clearings show many woodland species competing with the plants which always at first take possession of such deserted areas. Few, however, can adjust themselves to loss of light. When deprived of a large amount of light by the growth of the forest crown in density, only those species remain which are truly shade-loving. This difference of behavior explains why so few herbaceous plants are found beneath the dense shade of the hemlocks and rhododendrons. Mitchella repens,[27] Viola rotundifolia, Galax aphylla, Leptorchis liliifolia, Peramium pubescens, and Listera Smallii seem to be the more common plants tolerant of the shade of the forest. On the higher mountains, the coniferous forest acts in the same way, for when the dominant trees are removed, or the close crown broken, many herbaceous plants spring up and cover the ground.

Another noteworthy fact, which is of philosophic interest in

[26] Compare MACDOUGAL, D. T., The influence of light and darkness upon growth and development. Memoirs New York Bot. Garden **2**. 1902.

[27] The nomenclature used is that of Britton's *Manual*.

the discussion of the light-relationship of plants, is that many species which grow beneath the shade of a deciduous forest bloom in the early spring, and complete their most important vegetative and reproductive functions before the leaves of the trees above have fully unfolded. The boreal plants, however, which remained at the north during the glacial period, are an exception to this rule, for they owe their presence in the temperate forests and sphagnum bogs to the fact that they were trapped at the close of the glacial period by the northward-moving forest trees and had to adapt themselves to the changed conditions. Those boreal plants which did not do this were exterminated by the forest plants.

The density of the forests affords some indication of the general character of the flora. Upon the slopes of the southern Alleghenies the deciduous forest attains unsurpassed richness and variety. On the slopes of the high mountains of North Carolina and Tennessee the principal trees of the Appalachian forests attain their greatest size, and in a ride of a few hours, covering a rise in elevation of 4,000 to 6,000^{ft} (1220–1,525^{m}), one may see growing in perfection trees of the south, such as the magnolias; trees of the middle states, such as the ashes, the oaks, the maples, the lindens; and then the birches, the pines, the mountain ashes, and the spruces, of the extreme north.[28]

Climatic and edaphic considerations.—The differences in the character of the mountain region are not determined so largely by the kind of soil, or by the amount of moisture contained in it, as are those of the Piedmont plateau and the coastal region. Within short distances in the mountains are found wide variations in elevation. A rapid lowering of the average annual temperature takes place with the increased elevation, and a proportional shortening of the growing season; increase in the rainfall and relative humidity, and a decrease in evaporation both directly from the soil and through the foliage. It is noticeable that edaphic as well as climatic factors become more xerophytic

[28] Garden and Forest 5:155, 325; *cf.* PRICE, Practical forestry in the southern Appalachians. Yearbook U. S. Dept. Agric. 1900: 354.

upward.[29] The effect of climatic conditions on the higher mountains is more evident than that of soils; though between certain limits of elevation changes in the character of the soil influence the kind of growth. Thus the location of Rhododendron maximum and Tsuga canadensis along the mountain streams between certain limits of elevation (climatic) is regulated purely by edaphic conditions. The growth of Castanea dentata, Quercus alba, etc., back from the streams on the hillsides in the drier ground is also edaphic. The presence, therefore, of the various tree species in the mixed forests of the southern Appalachians is dependent primarily on climatic influences, but the assembling of these species into ecologic plant associations in these mixed deciduous forests depends upon the edaphic surroundings. With the herbaceous plants of the mountain summits and with certain shrubs, their allocation to particular situations on these summits is controlled mainly by edaphic conditions. Thus Dendrium buxifolium is found growing on rock faces and rocky slopes on Grandfather Mountain, while on Roan Mountain it is found in a deep soil, rich in humus. Xerophyllum asphodelioides, Gaultheria procumbens, Paronychia argyrocoma, Geum radiatum, etc., growing on Grandfather Mountain are controlled largely in their distribution upon that peak by soil conditions. Other examples of this kind of distribution might be mentioned here, but a more detailed reference will be made to the association of species in the forests of the higher mountains, when the several regions visited by the writer are discussed from an ecologic standpoint.

It is doubtful, however, if changes of soil in the larger mountain masses above 5,000^{ft} (1,525^{m}) elevation produce any change in the kind of trees, the number of species being limited to those whose hardiness (xerophytic structure of crown or foliage and short growing season) renders them capable of withstanding the sudden changes of temperature to which they are subjected near the summits of the higher mountains.[30]

[29] The word "xerophyte" refers to a particular kind of plant with a definite histologic structure. The word "xerophytic" should be used also in the structural sense, although by extension it is used loosely to denote conditions that produce xerophytes.

[30] PINCHOT and ASHE, Timber trees and forests of North Carolina. N. C. Geol. Survey 1897: 208, 209.

The forests of the mountain region of North Carolina are separable, according to Pinchot and Ashe, into three belts, lying at different elevations. These are as follows: (1) the forests of the lower mountains; (2) the forests of the higher mountains; (3) the forests of the mountain summits.

Zonally (climatically) the lower slopes of the mountains and valleys between are largely occupied by extensions of the Upper Austral (Carolinian) zone, but by far the greatest part of the surface of the mountain region is covered with an Alleghanian (Transition) flora. The higher mountains maintain Canadian trees, shrubs, and herbaceous plants, while along the crest of the highest mountains of this region, usually at an altitude of $6{,}000^{ft}$ ($1{,}830^{m}$) and upward, a sparse Hudsonian flora is encountered.[31] The green alder, Alnus alnobetula (allocated by edaphic conditions), Potentilla tridentata, Arenaria groenlandica, and Trisetum subspicatum may be regarded as typical of this zone.

Ecologically the following formations may be distinguished. Primarily these formations are determined by climatic conditions, and to give them ecologic significance they are named according to the character of the vegetation that determines them. The plant associations existing as part of these formations are determined largely by light and soil-moisture (edaphic) conditions. Tentatively, the ecologic formations and associations described in the following pages are these.

1. MIXED DECIDUOUS FOREST FORMATION ($2{,}000$–$5{,}000^{ft}$, 610–$1{,}525^{m}$).

Castanea-Quercus-Acer Association.
Tsuga Association.
Rhododendron maximum Association.
Lilium Association.
Plantago-Achillea Association.
Rubus Association.
Robinia hispida Association.
Aesculus-Acer-Betula Association.
Acer-Sorbus-Viburnum Association.
Betula-Fagus Association.
Aesculus Association.

2. CONIFEROUS FOREST FORMATION ($5{,}000$–$6{,}700^{ft}$, $1{,}525$–$2{,}040^{m}$).

Sorbus-Acer-Association (poorly defined).
Polytrichum-Hypnum Association.
Sedum-Carex Association.
Veratrum Association.
Rhododendron catawbiense Association.
Carex-Poa Association.
Picea-Abies-Prunus Association.
Viburnum-Vaccinium Association.

[31] The student is referred to a paper by KEARNEY (Science N. S. **12**: 830, 831) for the plants that characterize these zones.

3. SUB-ALPINE DWARF TREE-SHRUB FORMATION (circa 6,000^{ft}, 1,830^{m}).

Dendrium Association. *Geum-Paronychia Association.*

4. SUB-ALPINE TREELESS FORMATION (above 6,000^{ft}, 1,830^{m}).[32]

Rhododendron catawbiense Association. *Dendrium Association.*
Alnus Association. *Lycopodium-Geum Association.*
Carex-Poa Association. *Kneiffia-Hypericum Association.*
Polytrichum Association.

ECOLOGIC SURVEY OF THE REGION.

An ecologic survey of this region comprises a description of the flora of the north branch of the Swannanoa River and the slopes, ridges, and summits of Mount Mitchell and the mountains near it. The floras of the slopes and summit of Grandfather Mountain and of the summit and higher slopes of Roan Mountain are considered.

MIXED DECIDUOUS FOREST FORMATION.

The valley of the North Fork of the Swannanoa River is occupied by an arboreal vegetation, composed of Castanea dentata, Liriodendron tulipifera, Fagus americana, Quercus alba, Q. rubra, Magnolia acuminata, Juglans cinerea, Quercus coccinea, Q. phellos, Acer saccharum, Betula lenta (*Castanea-Acer-Quercus Association*).

These dominant trees are found somewhat back from the streams, while near the streams, with their roots in the water, or where the lower parts of their trunks may be submerged during heavy rains, grow Platanus occidentalis, Tsuga canadensis, Betula lenta (*Tsuga Association*).

In this forest, and belonging to the *Castanea-Quercus-Acer Association*, are these secondary species: Acer saccharum, Aesculus pavia, Juglans cinerea, Hamamelis virginiana, Hicoria glabra, Cornus florida, Tilia americana, Acer rubrum, Tilia heterophylla, Magnolia fraseri, Acer pennsylvanicum, and Robinia pseudacacia.

As a third lower story of the forest, the following species occur: Kalmia latifolia, Cornus florida, Cornus alternifolia, Ilex monticola, Oxydendrum arboreum, Viburnum acerifolium.

[32] Mount Mitchell does not show formations 3 and 4, while Roan Mountain shows all four well defined, Grandfather Mountain 3 and 4, but 4, if at all present, occupies a restricted area.

Rhododendron maximum forms a dense jungle along the borders of streams (*Rhododendron maximum Association*). Next to the secondary species mentioned above, the most important component of this forest is Rhododendron maximum, associated with Kalmia latifolia. The shade formed by these shrubs is so dense that few plants can exist in it. Saplings of Aesculus pavia, Fagus americana, and Tsuga canadensis, and a few herbs, such as Mitchella repens and Viola rotundifolia, seem to flourish, overshadowed by the laurel and rhododendron. Under the deciduous trees, where more light filters down to the forest floor, are found Podophyllum peltatum, Arisaema triphyllum, Cypripedium acaule, Cimicifuga racemosa, Sanguinaria canadensis, Euphorbia corollata, Lysimachia quadrifolia, Tradescantia montana, Galium latifolium, Pedicularis canadensis, Circaea lutetiana, Phytolacca decandra, Astilbe biternata, Mitchella repens, Scutellaria pilosa, Peramium pubescens, and such a sciaphilous[33] herb as Galax aphylla. Associated with these occur Silene virginica, Cacalia atriplicifolia, Zizia Bebbii, Lilium superbum in damp places (*Lilium Association*), with Thalictrum coriaceum. As lianes one finds Aristolochia macrophylla, Vitis aestivalis, Celastrus scandens, Smilax rotundifolia crenulata.

The dripping rocks, with damp soil pockets, support such plants as Trillium erectum, Salomonia biflora, Vagnera racemosa, Kneiffia fruticosa, Houstonia serpyllifolia, Thalictrum clavatum. In drier situations grow Caulophyllum thalictroides, Impatiens biflora, Adiantum pedatum, and Botrychium virginianum.

The clearings in the forest are tenanted by a number of introduced weeds, such as Chrysanthemum leucanthemum, Plantago lanceolata, P. Rugelii, Oxalis stricta, Trifolium repens, Carex rosea radiata, Achillea millefolium, Solanum carolinense, Arabis canadensis, Senecio aureus, and abandoned apple trees (*Plantago-Achillea Association*). Rubus strigosus forms dense bramble thickets in such areas (*Rubus Association*).

The dominant forest trees belonging to the Castanea-Quercus-Acer Association found on the slopes of Grandfather Mountain from an elevation of 3,800 to 4,500^{ft} (1,150–1,370^{m}) are Castanea

[33] POUND and CLEMENTS, The phytogeography of Nebraska, 166. 1900.

dentata, Quercus coccinea, Q. Phellos, Q. platanoides, Q. alba, Fagus americana, Magnolia acuminata, Robinia pseudacacia, Acer rubrum, Nyssa sp.; while as secondary species, usually found beneath the dominant ones, can be mentioned Prunus pennsylvanica, Rhododendron maximum, Hamamelis virginiana, and Kalmia latifolia. On this mountain the woody plants of less obvious importance, which may be considered to form a still lower story, are Pieris floribunda, Sassafras, and Robinia hispida, the last forming an almost pure growth (*Robinia hispida Association*). The herbaceous plants beneath the trees are Galax aphylla, Medeola virginiana, Diodia virginiana, Silene virginica, Pedicularis canadensis, Asclepias exaltata, Lysimachia quadrifolia, Osmunda cinnamomea, Dryopteris marginalis, Pteridium aquilinum, Uvularia puberula, Prunella vulgaris, Podophyllum peltatum, Ceanothus americanus, Monarda didyma, Chrysanthemum leucanthemum, Cerastium viscosum, Trifolium repens, and near cultivation Glechoma hederacea.

The forest on the northern slopes of Roan Mountain is similar to those on the Swannanoa River and Grandfather Mountain. It comprises the MIXED DECIDUOUS FORMATION with the *Castanea-Quercus-Acer Association*, as well characterized as at the places described above.

Reaching an elevation of 4,500^{ft} (1,370^{m}) on the Black Mountain Range, Picea mariana is found sparingly in the forest, as outposts of the main coniferous forest above. Associated in such places, the botanist finds as an indication of a rise in altitude, Diphylleia cymosa, Veratrum viride, Rhododendron lutea, Thalictrum clavatum, and an abundance of Houstonia serpyllifolia. As he approaches "Half Way" (5,200^{ft}, 1585^{m}) the forest of deciduous trees becomes more open by the lowering of the crown of the dominant trees (*Aesculus-Acer-Betula Association*) which are here Castanea dentata, with flat-topped crown, as an index of altitude, Quercus rubra, Q. coccinea, Aesculus pavia, Quercus alba, Acer saccharum, Betula lutea, and an occasional Picea mariana.

A somewhat different assemblage of species is found on Grandfather Mountain at an elevation above 4,500^{ft} (1,370^{m}). The

dominant species are Quercus rubra, Picea mariana, Acer saccharinum, Prunus pennsylvanicum on the drier soils, and Tsuga canadensis (*Tsuga Association*) ascending along the water courses to about $4{,}700^{ft}$ ($1{,}430^{m}$). The secondary species are Acer pennsylvanicum, Sorbus americana, Viburnum alnifolium, and Acer spicatum (*Acer-Sorbus-Viburnum Association*). The herbaceous plants of this part of the mountain have more light and comprise Osmunda cinnamomea, Pteridium aquilinum, Polygonum cilinode, Houstonia serpyllifolia, Podophyllum peltatum, Lysimachia quadrifolia, Saxifraga Michauxii, Rumex acetosella, and Chrysanthemum leucanthemum. Occurring as undershrubs are Rhododendron lutea, Ribes rotundifolium, and Viburnum alnifolium.

On Roan Mountain the first indication of rise in altitude is furnished by Acer spicatum, and then by Acer pennsylvanicum, which does not descend quite so low as the mountain maple. Viburnum alnifolium occurs in great abundance when at an altitude of $4{,}500^{ft}$ ($1{,}370^{m}$) is reached. Houstonia serpyllifolia carpets the ground in many places, while in damp places Diphylleia cymosa forms masses beneath the shade of the dominant forest trees. The herbaceous plants of the forest floor at this elevation are Caulophyllum thalictroides, Actaea alba, Cicimifuga racemosa, Tiarella cordifolia, Sanguinaria canadensis, Podophyllum peltatum, Circaea alpina, Blephariglottis peramoena, Cacalia atriplicifolia, Lysias orbiculata, Chelone Lyoni, and Polystichum acrostichoides. A few straggling black spruce trees descend the mountain side and mingle with Betula lutea and B. lenta. Fagus americana, which becomes dwarfed at the edge of the coniferous belt, is associated with the birches in this tension zone (*Betula-Fagus Association*).

Aesculus octandra, which occurs at the upper edge of the tension zone, ascends the mountain into Carver's Gap, where it forms an almost pure stand of gnarled trees (*Aesculus Association*).

CONIFEROUS FOREST FORMATION.

The coniferous forest appears on the slopes of the Black Mountain Range at about $5{,}200^{ft}$ ($1{,}585^{m}$). The dominant tree of this formation is Picea mariana, associated with Abies Fraseri. Intermingled with these two coniferous trees, but nowhere mak-

ing a pure growth, are Acer spicatum, Betula lutea, Aesculus flava, Sorbus americana, and Crataegus sp. (*Sorbus-Acer Association*). The trees are large and rugged, and clothed even to the topmost branches with dense coats of moss. Mosses and lichens cover the ground as with a dense mat a foot or more thick. The trunks of fallen trees are buried from sight by a living mound of green, set with flowers and ferns. The mosses and lichens collected by the writer, which form the *Polytrichum-Hypnum Association* on Potato Top and Clingmans Dome comprises the following: Polytrichum gracile, Sematophyllum delicatulum, Hypnum fertile, Hylocomium proliferum, Bazzania trilobata, Hylocomium triquetrum, Dicranum fuscescens, Hypnum reptile, Polytrichum ohioense, and Stereocaulon coralloides. Associated with these mosses are herbaceous plants and ferns, viz., Oxalis acetosella, Viola blanda, Lycopodium lucidulum, and Aspidium spinulosum intermedium. Houstonia serpyllifolia is also abundant. The rocks support in sunny places Sedum and telephioides, Carex rosea radiata, Saxifraga leucanthemifolia, Krigia montana (*Sedum-Carex Association*).

The green hellebore is found wherever the timber is more open and in extensive patches many square feet in area (*Veratrum Association*). The same association of species extends to the tops of the several mountains composing the Black Mountain Range. Acer spicatum and Sorbus americana (*Sorbus-Acer Association*) are met with in this forest belt. Many seedling spruces are providing a natural regeneration of the forest. As a secondary but important element of this belt at high elevations, is the Rhododendron catawbiense, beneath which as herbaceous associates are found Viola blanda, Trillium erectum, and Clintonia borealis (*Rhododendron catawbiense Association*).

The natural meadows on this range of mountains, surrounded by the forest of balsam and black spruce trees, are composed of such species as Carex intumescens, Juncus effusus, Carex scoparia, C. brunnescens gracilior, C. tenuis, Poa pratensis, Agrostis alba, Poa alsodes, Juncoides bulbifera (*Carex-Poa Association*).

The coniferous forest extends to the summit of Mount Mitchell $6{,}711^{ft}$ ($2{,}045^{m}$) without any indication of subalpine or alpine

conditions. Wind-tossed specimens of Picea mariana, Abies Fraseri (*Picea-Abies-Prunus Association*), are seen. Huge rocks and bowlders project from the rounded dome. Menziesia pilosa, Ribes prostratum, Sorbus americana are common. Rhododendron catawbiense grows within a few feet of the Mitchell monument. The herbaceous plants of the summit are Streptopus roseus, Scirpus caespitosus, Carex brunnescens, Houstonia serpyllifolia Rumex acetosella, Trifolium repens, Asplenium filix-foemina, Saxifraga Michauxii in the crevices of the rocks, and Clintonia borealis. None of these herbs are true alpines.

Mosses are found on the trunks of trees and on the rocks, the following being noted:[34] Ulota crispa, Bryum nutans, Sematophyllum delicatulum, Hylocomium proliferum, Polytrichum gracile, Hypnum Schreberi (*Polytrichum-Hypnum Association*). The trees of the summit are Picea mariana, Abies Fraseri, Betula lutea, Prunus pennsylvanica.

The coniferous forest on Grandfather Mountain consists essentially of the same arborescent species, viz., black spruce and balsam. Associated with these are Viburnum alnifolium, Vaccinium stamineum, Acer spicatum, and Rhododendron catawbiense (*Viburnum-Vaccinium Association*). Polypodium vulgare grows in masses, associated with Galax aphylla, Oxalis acetosella, Thalictrum clavatum, Maianthemum canadensis, and Clintonia borealis.

The forest of cone bearers on the higher elevations of Roan Mountain consists of Picea mariana and Abies Fraseri as the dominant trees. Intermixed with these, but never forming pure growths, occur Aesculus octandra, Sorbus americana, Fagus americana in a dwarfed form, and as a third lower story, Ribes rotundifolium, Cornus atternifolia, and Alnus alnobetula. The forest floor, beneath the shade of the dominant trees, supports seedling conifers, Circaea alpina, Veratrum viride, Oxalis acetosella, Viola blanda, Thalictrum clavatum, Polypodium vulgare, Asplenium filix-foemina, Dryopteris spinulosa dilatata, Houstonia serpyllifolia, Tiarella cordifolia, and Clintonia borealis.

[34] The identification of the mosses I owe to Mrs. Elizabeth G. Britton and that of the flowering plants to Dr. John K. Small, to whom my thanks are due.

SUB-ALPINE DWARF TREE-SHRUB FORMATION.

This formation may be said to exist only at the top of Grandfather Mountain and is absent from the domes and ranges of Mount Mitchell and Roan Mountain.

The summit of the west peak of Grandfather Mountain for a limited area is bare and presents an alpine aspect, being clothed with lichens, mosses, and dense cushions of Dendrium buxifolium (*Dendrium Association*). Several of the plants remind the botanist of the New Jersey pine barrens, viz., Gaultheria procumbens, Xerophyllum asphodelioides, Pteridium aquilinum, Kalmia latifolia.

Zygadenus leimanthoides, Geum radiatum, Paronychia argyrocoma, Uvularia puberula, Clintonia borealis, Carex aestivalis, Chrosperma muscaetoxicum, and Solidago spithamea are found in exposed places (thus under edaphic conditions) (*Geum-Paronychia Association*). Abies Fraseri, Picea mariana, Clethra acuminata, Sorbus americana, Leucothoe recurva, Vaccinium pallidum, Oxycoccus erythrocarpus accompany the herbs to the mountain summit, so that this summit may be said not to be entirely treeless, otherwise the plants on it would be classed as an association of the Sub-alpine Treeless Formation.

The presence of Dendrim buxifolium, Xerophyllum asphodelioides, a pine barren species found plentifully in New Jersey, Geum radiatum, Paronychia argyrocoma, Clintonia borealis, and Chrosperma muscaetoxicum needs explanation. Paronychia argyrocoma, found on the bare mountain slopes of the White Mountains and in the Alleghenies from Virginia to Georgia and also in Maine, and Clintonia borealis are probably species of north temperate habit that were formerly more widely distributed but have been separated into distinct areas by the influence of the base-leveling operations previously described.

The geographic distribution of Xerophyllum asphodelioides and Chrosperma muscaetoxicum is probably to be accounted for in the same manner as the distribution of the austro-riparian species that occur in the southern Appalachians. It is hardly likely that the seeds of these plants were carried to the summit of the few isolated peaks by birds, because one would expect to

find them in intermediate situations. Another explanation must be appealed to. It is probably found in the uplift at the close of the Cretaceous period, followed by the subsequent base-leveling operations. While the eastern United States, including that part of New Jersey along the Delaware River, was an almost featureless peneplain during the close of the Cretaceous, it is conceivable that the plants above mentioned had a more general distribution, and that when the uplift of the Appalachian system occurred and the formation of the Tertiary coastal plain was well under way, these plants, then widely distributed, were subjected to the influences of the processes of gradation. The wearing away of the soil from the mountains, the formation of valleys, and the oscillations of the coast line led to a process of extermination, and many plants succumbed in those regions to the geologic changes. The survivors of many widely distributed groups of plants are found, therefore, in those places that resisted the action of the destructive forces, such as the present summits of high mountains, or are in regions not subjected to the oscillations in level of the coastal plain. This supposition is supported by the suggestion of Cowles, that in all probability these plants survive under such conditions because the summits of these mountains and the sandy coastal plain are in about the same stages of their life histories. It seems to the writer, that the similarity of the situations, which are in the same edaphic stage of their life histories, consists in this.[35] In the dry places, especially the insolated slopes of the high mountains, the humus is sour or "raw;" in fact, the dense tangle which roots often form in such situations is well known for its tendency to produce sourness by hindering aeration. Similar sour humus is found in the wet swampy forests. Sour humus makes it more difficult for the roots to absorb moisture, and consequently it becomes necessary for the plant to reduce transpiration. The lack of oxygen and assimilable forms of nitrogen in such soils still further induces a weakening of physiologic activity. It appears clear, therefore, that the number and importance of xerophilous conditions increases in

[35] This thought was suggested by a reading of a paper by ERNEST BRUNCKEN, Contributions to the ecology of the genus Viola. Bull. Wis. Nat. Hist. Soc. 2:27.

inverse proportion to the presence of fresh well-aerated humus. Does not this circumstance seem to imply that there must be some causal connection between the quality of the humus and the occurrence of xerophytic characters? The presence of such plants as Xerophyllum asphodelioides, Paronychia argyrocoma, Chrosperma muscaetoxicum on the summit of Grandfather Mountain, and Dendrium on both Grandfather and Roan Mountains seems thus to be explained.

SUB-ALPINE TREELESS FORMATION.

This formation is encountered typically on Roan Mountain and on other mountain summits in the southern Appalachians that are grassy balds. The "balds" are in the main grassy meadows, but the rounded domes show extensive areas covered by the Rhododendron catawbiense (*R. catawbiense Association*), either pure, or associated with Alnus alnobetula (*Alnus Association*). The alder covers an adjoining dome of the Roan Mountain Range, the Elkhorn, with a pure and impenetrable growth three to four feet high. The extent of the rhododendron thickets, for which the mountains is famous, cannot easily be estimated. The bushes may be either rounded, like a hay stack, or they may be spreading at the top.[36] The character of the plants, as indicated by the general habit and nature of the leaves, depends upon whether the plants are exposed to the cold winds of summer, the intense sunlight, the icy blasts of winter, or whether they are more or less sheltered by the slope of the ground, or by growing beneath the protection of the spruces and silver firs.

The summit of Roan Mountain is in the form of a saddle several miles long, being formed of two elevations of about equal height, the culminating peak being $6,313^{ft}$ ($1,924^{m}$) in altitude. The component vegetation of the grassy meadows, or "balds" consists of Trifolium repens, Rumex acetosella, Potentilla canadensis, Poa compressa, Veronica officinalis, Houstonia serpyllifolia, Carex tenuis, Deschampsia flexuosa, Luzula campestris, and Phleum pratense (*Carex-Poa Association*). Polytrichum com-

[36] *Cf.* CANNON, W. A., Field notes on *Rhododendron Catawbiense*. Torreya 2:161. 1902.

mune forms patches, especially about old stumps (*Polytrichum Association*).

The raised cushions of soil found here are covered by various mosses, or by Dendrium buxifolium[37] (*Dendrium Association*). In or along the dry stony wash-ways, one finds Saxifraga leucanthemifolia, Potentilla tridentata, and Houstonia purpurea.

The immediate summit of Roan Mountain is characterized by the presence of Geum radiatum, Lycopodium selago (*Lycopodium-Geum Association*), Menziesia pilosa, Houstonia purpurea, Lycopodium lucidulum, Ribes rotundifolium, Dendrium buxifolium. Alnus alnobetula clings to the north slopes, here forming a pure growth on the steeper inclines (*Alnus Association*), with Sorbus americana below it, but associated with Rhododendron catawbiense on the upper slopes of the dome.

Crossing Carvers Gap, where Aesculus octandra grows (*Aesculus Association*), a rocky outcrop is found on the slope of Little Roan Mountain where the writer collected Rhododendron lutea, Kneiffia fruticosa, Geum geniculatum, Arisaema quinatum and Hypericum graveolens (*Kneiffia-Hypericum Association*). Alder Bald or Elkhorn, as it is called, is reached from Little Roan Mountain by crossing a smaller wind gap. The slopes of this knob are covered by acres of Alnus alnobetula (*Alnus Association*), while the stony places are favorable for the growth of Heuchera villosa, Krigia montana, Cerastium vulgatum, and two alpine species, Potentilla tridentata and Alsine groenlandica. The latter herb assumes the cespitose character in exposed situations.

In conclusion, it is advisable to state that the dwarfing of the trees and their absence on the "balds" is explicable by the action of winter storms which beat upon these summits. Wherever the topography is such as to permit the full force of the ice storm, there tree vegetation is scanty or altogether wanting, and its place is taken by grassy stretches, or by thickets of alder and rhododendron, plants which are adapted to withstand ice storms.[38]

[37] *Cf.* SMALL, J. K., Flora of western North Carolina and contiguous territory. Mem. Torr. Bot. Club 3.

[38] HARSHBERGER, J. W., Thermotropic movements in the leaves of *Rhododendron maximum* L. Proc. Acad. Nat. Sci. Philadelphia 1899 : 219.

Mrs. Edson[39] describes the action of a winter storm upon the vegetation. The factor in the production of the frost forms which weigh down the limbs of trees and snap them off is the frozen vapor of the wind and rain. The lower the temperature, the denser the cloud becomes; the velocity of the wind and the exposure determine the growth of the frost forms. Hence the absence of trees is due to the effect of the ice and snow of winter. This conclusion is strengthened by a study of a recent ice storm at Philadelphia,[40] as it damaged large trees that had withstood the storms of centuries.

In lieu of illustrations to accompany this article, the reader is referred to a magnificent volume issued by the United States Government,[41] where maps and photographs descriptive of the proposed Appalachian National Park are given.

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[39] EDSON, Mrs. HELEN R., Frost forms on Roan Mountain. Pop. Sci. Mo. 45:30. 1894.

[40] Forest Leaves 8:168. 1902; also CHAPMAN, Forestry and Irrigation 8:130. 1902; Experiment Station Record 13:1053.

[41] See Message from the President of the United States transmitting a Report of the Secretary of Agriculture in relation to the forests, rivers, and mountains of the southern Appalachian region. Senate Document 84:210. Washington. 1902.

BRIEFER ARTICLES.

THE MITOSES IN THE SPORE MOTHER-CELL OF PALLAVICINIA.

(WITH SIX FIGURES)

In 1894 Farmer published a paper[1] on *Pallavicinia decipiens* reporting the occurrence of very peculiar phenomena in the division of the spore mother-cell. According to his account the nucleus in preparation for division is surrounded by dense protoplasm which projects into each of the four lobes of the mother-cell and forms a four-rayed star. He termed this structure a "quadripolar spindle." After the formation of the "quadripolar spindle," four chromatic droplets make their appearance in the nucleus as the first positive evidence of approaching division. The four chromatic droplets become four chromosomes, which by division are doubled in number. The resulting eight rod-shaped chromosomes point off in pairs towards the four lobes of the spore mother-cell. Further doubling takes place, increasing the total number of chromosomes to sixteen, and four chromosomes pass simultaneously to each pole of the four-rayed spindle, which persists to the end.

Farmer's later studies[2] on other Jungermanniales revealed the presence of the "quadripolar spindle" in the early stages of mitosis, but in no case did he find a repetition of the peculiar conditions described for Pallavicinia. In all other forms the "quadripolar spindle" is a temporary structure, which is later replaced by normal bipolar spindles of two successive mitoses with longer or shorter intervals between. Farmer interprets the temporary four-rayed star of these plants as transitional between the "quadripolar spindle" of Pallavicinia and the normal bipolar spindle.

Davis in 1901 described[3] conditions during spindle formation in the spore mother-cell of *Pellia epiphylla* substantially in agreement

[1] FARMER, Studies in Hepaticae: On *Pallavicinia decipiens* Mitten. Ann. Botany 8:35. 1894.

[2] FARMER, On spore formation and nuclear division in the Hepaticae. Ann. Botany 9:363 and 469. 1895.

[3] DAVIS, Nuclear studies on Pellia. Ann. Botany 15:147. 1901.

with Farmer's studies on the same form, but the two observers differ widely in their interpretation of the facts. Davis considers Farmer's "quadripolar spindle" as a transitory stage of prophase, which should not be regarded as a part of the true spindle that is formed later. The nuclear divisions in the spore mother-cell of Pellia are effected by two successive mitoses, each with a bipolar spindle and the gametophytic number of chromosomes (eight) at the nuclear plate of each metaphase. There is also a well-defined period between the two mitoses when the nuclei are in the resting condition. The events of sporogenesis for Pellia are then essentially the same as those throughout the pteridophytes and in the development of pollen.

The striking peculiarities of Farmer's account of Pallavicinia lie not so much in the presence of a four-rayed achromatic figure as in the reported division of four primary chromosomes into sixteen, and their distribution to form simultaneously four daughter nuclei through the "quadripolar spindle." It is necessary to emphasize this point, since Farmer[4] in a criticism of Davis's paper on Pellia does not consider this matter, while taking exception to Davis's use of the term spindle. Davis found a four-rayed figure during prophase in Pellia, but was not willing to call it a spindle, since the actual distribution of the chromatin takes place in the usual manner at a later period through two successive mitoses, whose spindles are bipolar. The four-rayed structure in Pellia seems to Davis a character of prophase, determined largely by the peculiar crowded condition of the nucleus in the center of a four-lobed cell.

However, Farmer's very positive assertion of the persistence of the four-poled spindle, and his detailed account of the peculiar arrangement of the chromosomes and their simultaneous passage to the four poles in Pallavicinia, makes his position a strong one to assail except upon a reexamination of the conditions in Pallavicinia itself.

I am now at work on *Pallavicinia Lyellii* S. F. Gray, which is abundant in this locality. My studies are by no means complete, but have been carried far enough to justify conclusions on the chief events of sporogenesis, which are presented in this note. I have had the opportunity during past summers at Woods Hole of examining Dr. Davis's preparations of Pellia and have had the benefit of his suggestions and criticisms on technique.

In preparing for mitosis the nucleus of the spore mother-cell

[4] FARMER, The quadripolar spindle in the spore mother-cell of *Pellia epiphylla*. Ann. Botany 15:431. 1901.

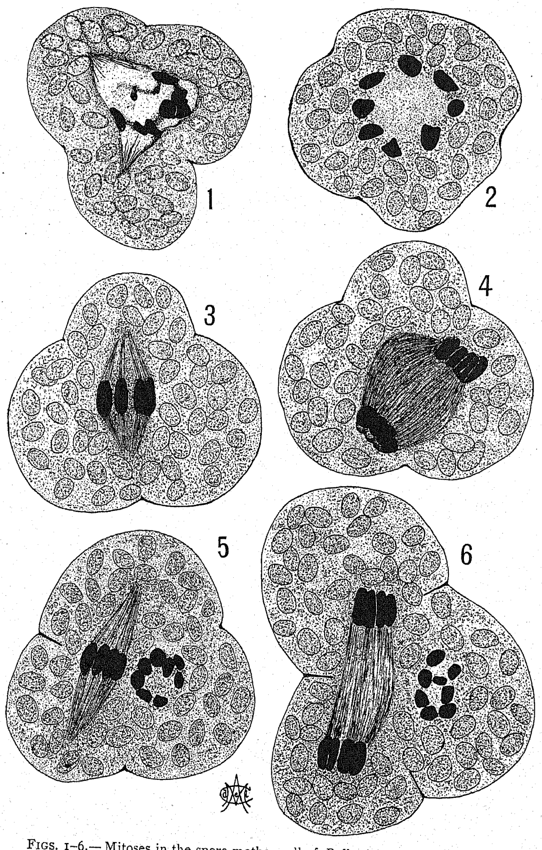
assumes a tetrahedral form, each angle of which points into one of the four lobes of the spore mother-cell. This form persists through synapsis and the spirem condition, and only disappears with the formation of the spindle.

While the chromosomes are being differentiated, and while there is still a trace of linin connecting them, fibers may be seen extending over the points of the tetrahedral nucleus as caps and into the nuclear cavity (*fig. 1*). With the appearance of these fibers the nuclear membrane becomes less distinct, some of the fibers finally occupying the position which it formerly held. During this period the incompletely differentiated chromosomes lie scattered irregularly throughout the interior of the nucleus.

With the complete disappearance of the nuclear membrane and the further growth of the fibers, this four-rayed structure rapidly passes over into a bipolar spindle and the chromosomes, eight in number, become clearly grouped in a ring to form the nuclear plate (*fig. 2*). I have found no evidence of their quadrupling in number, as was so positively asserted by Farmer. It is difficult to follow the development of the bipolar spindle from the four-rayed structure of prophase because the figure is small, but there is probably a rearrangement of the elements through the establishment of a single axis, around which the fibers and chromosomes become grouped.

Now follow two divisions in rapid succession without an intervening resting condition. There is no four-poled spindle in Farmer's sense, but well-organized bipolar spindles without centrospheres, and the chromosomes are distributed in the usual manner. *Fig. 3* illustrates the metaphase of the first division and *fig. 4* shows anaphase of the same. In the latter case the daughter chromosomes are seen to be grouped in a ring at the poles of the spindle. There appears to be no resting period. The second division begins immediately, the rings of chromosomes altering their positions so that their planes lie at right angles. Two distinct spindles are organized, their axes being perpendicular to each other. *Fig. 5* presents the conditions at metaphase of the second division and *fig. 6* illustrates anaphase when the mitoses of the spore mother-cell are completed. It should be noted that the two spindles of the second mitosis are entirely distinct from each other. My preparations show hundreds of examples similar to the stages that I have figured.

It will be seen that the foregoing account agrees substantially with



FIGS. 1–6.— Mitoses in the spore mother-cell of *Pallavicinia Lyellii*. For details see explanation on next page.

that of Davis for *Pellia epiphylla*, with the exception that in Pallavicinia there is no period of rest between the first and second mitoses.

I have carefully followed the nucleus of the spore mother-cell through all stages, from synapsis to the completion of the resting nuclei of the spores, and find that the only structure which could possibly be interpreted as a "quadripolar spindle" is that illustrated in *fig. 1*, which is clearly a condition of prophase. It does suggest Farmer's description of a "quadripolar spindle," and would be so interpreted but for the fact that it is followed by bipolar spindles of the normal type, through which the chromosomes are distributed by two successive mitoses in the usual manner. There is no quadrupling of the primary chromosomes or their simultaneous distribution in four groups to form the four daughter nuclei, which are the most remarkable features of Farmer's account of the activities of a "quadripolar spindle."

The number of chromosomes in *Pallavicinia Lyellii* differs from that reported by Farmer for *Pallavicinia decipiens*. He states that there are four in the gametophyte and eight in the sporophyte. I have not determined the number in the sporophyte, but find eight present in each mitosis in the spore mother-cell. This fact is clearly shown in the accompanying figures.

I hope soon to present a more detailed account of these events of sporogenesis, together with nuclear studies upon other phases in the life history of *Pallavicinia Lyellii*.—ANDREW C. MOORE, *South Carolina College, Columbia.*

EXPLANATION OF FIGURES 1–6.

FIG. 1. Prophase of the first mitosis; the nucleus has a tetrahedral form, the points being directed into the four lobes of the spore mother-cell; fibrillae are gathered at these points but the nuclear membrane has not yet broken down; similar stages of prophase were probably considered by Farmer as quadripolar spindles.

FIG. 2. The eight chromosomes, grouped in a ring at the nuclear plate, are viewed from above.

FIG. 3. Metaphase of the first mitosis; the spindle in all respects a normal bipolar structure without centrospheres.

FIG. 4. Anaphase of the first mitosis.

FIG. 5. Metaphase of the second mitosis; one spindle seen from the side; the other, almost perpendicular to the first, shows the eight chromosomes at the nuclear plate.

FIG. 6. Anaphase of the second mitosis; one spindle seen from the side; the other seen from one end shows a group of eight grand-daughter chromosomes.

IS DETMER'S EXPERIMENT TO SHOW THE NEED OF LIGHT IN STARCH-MAKING RELIABLE?

(WITH TWO FIGURES)

IN HIS *Practical Plant Physiology*,[5] Detmer's method of showing the necessity of light in photosynthesis, is to pin disks of either card board or felt, exactly opposite, on both sides of a tropaeolum leaf.[6] With the exception of the area covered starch forms throughout the entire leaf. This experiment, slightly modified by using cork in place of felt or cardboard, is found in several school text-books. While performing this experiment as given in one of these books, the question arose whether the cork did not so hinder the diffusion of CO_2 that the failure to form starch was not entirely due to the absence of light.

First, some students performed a number of experiments,[7] but as they did not derive conclusive results, at the suggestion of Mr. L. Murbach and with aid from him, I made further experiments.

It is not stated in most of the ordinary text-books that the small percentage of carbon dioxid in the air does not diffuse extensively through the intercellular spaces in leaves, though it may be inferred from experiments given in a number of standard handbooks.

It is well known that the formation of starch is prevented when the leaf surface bearing stomata is smeared with vaseline, paraffin, or cocoa butter, and if only a portion of the leaf is so smeared starch appears for the most part or entirely in the unsmeared regions. This I verified in *Primula obconica* by using melted paraffin (nearly cold) for closing the stomata, which in this species are on the under surface only. The fact that starch forms when the upper epidermis is coated with paraffin shows that the warm paraffin has not injured the leaf. On the other hand, since light was admitted when the paraffin was placed on the under surface and no starch deposited, its absence can only be due to lack of carbon dioxid, and if it diffused far through the intercellular spaces, the formation of starch would still be possible. It is evident, then, that diffusion of carbon dioxid is not very extensive in the intercellular spaces of the leaf.[8]

[5] Pflanzenphysiologisches Praktikum 44. Moor, Eng. tr. 52.

[6] It should be noted that this method of fastening disks of any kind on the leaf necessitates pressing them very close to the surface.

[7] The most striking of these was with a perforated piece of cork held to the under side of the leaf by strips of cork on the upper surface. Starch formed only over the opening in the under cork.

[8] In normal leaves it need be only from stoma to stoma, or the equivalent distance in the intercellular spaces.

To determine whether the free access of air is prevented by corks or disks such as were used in Detmer's experiment, it is sufficient to close the stomata in a similar manner and still admit light. This was done by pinning only a narrow ring of cork, in place of the whole disk, on the upper surface of the Primula leaf, exactly opposite the disk on the lower surface. By this device light is admitted and the external approach to the stomata is obstructed.

The veins of the primula leaf, especially near the petiole, are much more prominent than those of tropaeolum, so the position of the

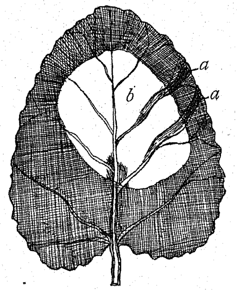


FIG. 1.—Leaf of *Primula obconica;* *a*, *a*, folds which admitted CO_2; *b*, space enclosed by cork.

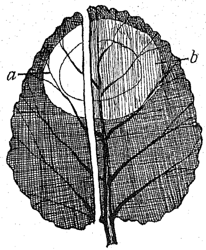


FIG. 2.—The same; *a*, area covered by cork disk on lower surface and enclosed by cork ring on upper; *b*, after forty minutes exposure uncovered.

cork must be near the margin of the leaf to make the experiment differ as little as may be from the original. In the first experiments the upper cork was placed over the larger veins, leaving some space for the circulation of air and as a result starch was deposited along these veins (*fig. 1*).

Still attached to the plant and with the corks adjusted, the upper one being only a ring, as described above, another leaf was placed in diffuse light two days, then in direct sunlight forty minutes. After removing the cork half of the leaf was cut off, the cut passing through the covered part (*fig. 2*); the half remaining on the plant was left in the sun forty minutes longer. In the part first removed there was no starch in the portion enclosed by the ring of cork (*a*, *fig. 2*), while in the second half, which was left without corks in the light forty minutes longer, there was considerable starch in the corresponding area.

(*b*, *fig.* 2). This was sufficient to prove that the tissues had not been injured, for in the time allowed they could scarcely have recovered from any injury that might have been received from the heat.[9] This was further affirmed by repetitions of the experiment, which gave only slightly varying results, and also by the fact that sometimes a small amount of starch was found in the whole area that had been enclosed by the cork, but never much in comparison with the amount found in other portions of the leaf.

The slightly different results obtained are easily explained by the fact that the corks, each time, may not have been fastened equally tight, or the veins may not have been of the same prominence, thus affording admittance to varying amounts of air.

In considering the facts brought out by these experiments, that when light is admitted to a leaf and at the same time the surface with the stomata is covered by a rather closely fitting object, and starch does not form, it seems evident that the cover hinders the free diffusion of CO_2. The experiment, as usually given, therefore, is not reliable. Disks of paper or cork, if used at all, should be attached so loosely that they do not obstruct the free access of CO_2 to the stomata.—BERNICE L. HAUG, *Detroit, Mich.*

[9] The fact that starch formed along some of the veins or along a fold in the leaf, or when the cork was not tightly appressed, also shows that the tissues were not injured.

CURRENT LITERATURE.

BOOK REVIEWS.

Botany of the Faeroes.

THESE INTERESTING ISLANDS have been the subject of a thorough investigation by Danish botanists, whose results are being published in English.[1] In part I Warming gives a brief account of previous botanical work in the islands, after which C. H. Ostenfeld sets forth the geography, topography, industrial conditions, geology, and climate. The latter author lists and discusses the phanerogams and pteridophytes of the islands, and presents an interesting phytogeographic summary. He finds, as have others in northern lands, that several species, more at home in temperate climes, do not bear fruit. There are no endemic species, and the flora is strikingly like that of Scandinavia and Britain. Of 277 species of vascular plants, 70 are Arctic, 164 Temperate European, and 43 Atlantic. Ostenfeld regards the flora as postglacial, and he thinks that the Faeroes have been joined to the continent since the ice age. The plants are not notably adapted for wind or bird dispersal; furthermore, few migratory birds pass over these islands; and those which come migrate on empty stomachs. The ocean currents have the wrong direction to be of any avail. Finally, there is good direct evidence of higher land in recent times. C. Jensen treats the bryophytes in a similar manner, and F. Börgesen takes up the freshwater algae. The latter author takes issue with Ostenfeld, and inclines to think that winds and migrating birds have brought most of the freshwater algae to the islands. Jan Mayen has similar facts to be accounted for, but there a postglacial land bridge is out of the question. E. Östrup treats the freshwater diatoms, E. Rostrup the fungi, and Deichmann Branth the lichens.

Most of part II is taken up by Börgesen's excellent treatment of the marine algae. He lists and discusses critically 83 reds, 73 browns, 46 greens, and 14 blue-greens. Östrup considers the marine diatoms, and Ostenfeld the marine phytoplankton. The latter author discusses the seasonal changes of the plankton, which he finds to be prevailingly oceanic and not arctic in relationship. The phytoplankton of freshwater lakes is presented by Börgesen and Ostenfeld, and Dahlstedt gives a critical account of the Hieracia. At the close of the second part Warming considers the question over which Börgesen and Ostenfeld disagreed in the first part, and

[1] BOTANY of the Faeroes based upon Danish investigations. Part I. 8vo. pp. 338. *pls. 10. figs. 50.* 1901. Part II. pp. 343. *pls. 2. figs. 100.* 1903. Copenhagen: Det Nordiske Forlag; London: John Wheldon & Co.

he is inclined to side with Börgesen. The Faeroes certainly have a flora of recent origin, thus contrasting with the Azores and Canaries, where endemism is to be found. While Warming accepts Ostenfeld's strictures in the matter of seed dispersal by birds and ocean currents, he thinks that wind is an adequate transporting factor. The fauna and geological considerations seem to unite against the land-bridge theory. Warming says that he is more inclined now than ever before to believe in the efficiency of wind as an agent for scattering seeds over great distances. A third and final part of this valuable work is promised for the near future.— H. C. COWLES.

Two text-books on agriculture.

AGRICULTURE FOR BEGINNERS, by Burkett, Stevens, and Hill[2] forms a small but very attractive volume, designed as a text-book in agriculture for the public schools. The subject-matter of the book is divided into nine chapters, each dealing with a subdivision of agriculture or related sciences, as: soil, diseases of plants, domestic animals, etc. If, as the authors believe, "agriculture is an eminently teachable subject" and should be taught in public schools, this book forms an excellent introduction to the subject. It is written in clear style and is remarkably free from errors which usually find their way into works dealing with such heterogeneous subjects as the so-called science of agriculture. Moreover, the excellent typography and numerous artistic illustrations make the little book unusually attractive. In a few cases it would seem that subjects are not treated in just proportion to their relative importance. Thus, the discussion of drainage of the soil is limited almost to bare statements of the effects of draining, without sufficient explanation to make them clear. On the other hand, two whole chapters are devoted to descriptions of specific fungous diseases and insect enemies, although these are hardly germane to the subject. The authors inform us that the chapter on dairying, in which accidentally were included several miscellaneous sections, has been properly rearranged in later impressions.

The other volume, entitled *Agriculture for the common schools*,[3] comes from the pen of James B. Hunnicutt. While this book contains an abundance of wholesome ethical advice and perhaps some good practical hints for the farmer, its absolute lack of scientific accuracy should preclude its use in the schoolroom. Aside from the general ignorance of natural phenomena displayed throughout the book, such flagrant errors as the following are common: "Each of these [roots] carries a little soft point called spongiole on the tip, and through this constantly absorbs or drinks in the water from the earth." "Some of these elements, such as carbon dioxid and hydrogen, were

[2] BURKETT, C. W., STEVENS, F. L., and HILL, D. H., Agriculture for beginners. pp. i + 267. *figs. 215.* Boston: Ginn & Co. 1903. $0.85.

[3] HUNNICUTT, J. B., Agriculture for the common schools. pp. viii + 225. Atlanta: The Cultivator Publishing Co. 1903.

formerly thought to be absorbed or taken into the plant through the leaves. . . . . It is now thought that even the air must furnish its food to plants through the roots."—H. HASSELBRING.

Biology of plants.

ONE OF THE first to appreciate the modern ecological view-point was Professor Wiesner, who issued his classical *Biologie der Pflanzen* in 1889. A second edition of this work has appeared[4] in which no radical change of treatment is to be seen. Throughout the new edition, however, the contributions of the past decade are found intercalated in their proper places. In the introduction there is a fuller setting forth of vitalism and mechanism. Among the topics which are added or much changed are polarity, light and rain adaptations, photometry (the author's own work). The chapter on evolution is also much changed, and the last part is largely new. The order of the chapters is as follows: SECTION I, Biology of the vegetative processes: the individual; survey of the plant forms according to their mode of life (biological types); primordia, development, form and direction of organs; polarity, correlations, and leaf position; complications in determining the causes of organic forms; rhythm of the vegetative processes; germination of seeds and buds; vegetative growth; flowering and fruiting; rest periods and leaf-fall; adaptation of plants to external vegetative conditions; adaptation of plants to other organisms; specific adaptations, reproduction; life duration; vitality. SECTION II, Biological relations of reproduction; distribution of sexual organs; wind-pollinated plants; insect pollinated plants; other aids to pollination, and transitions from one form to another; reciprocal pollination; adaptations for self-pollination; protective adaptations of flowers; apogamy. SECTION III, Distribution of plants; fundamental principles and problems; vegetation forms and formations; distribution areas of species, genera and families; principles of systematic phytogeography. SECTION IV, Development of the plant world (theory of descent). APPENDIX: Historical development of botany. Thus one may see how thorough and comprehensive is this admirable treatise on plant biology, or, as we would say, ecology.—H. C. COWLES.

Plant geography.

THE SIXTH volume of the invaluable series, *Vegetation der Erde*, is by Drude himself and embraces much of the material which he has been gathering for years in his own home-land of Saxony.[5] Just as Graebner's work on

[4] WIESNER, JULIUS, Biologie der Pflanzen, mit einem Anhang: die historische Entwicklung der Botanik. Zweite, vermehrte und verbesserte Auflage. 8vo. pp. viii + 340. *figs. 78* and *1 map*. Vienna: Alfred Hölder. 1902.

[5] DRUDE, O., Der Hercynische Florenbezirk. 8vo. pp. xix + 671. *pls. 5. figs. 16. 1 map*. Leipzig; Wilhelm Engelmann. 1902. *M*30, bound *M*31.50; to subscribers *M*20–21.50.

the heath[6] was the first of an ecological series on the formations of central Europe, so Drude's contribution is the first of a floristic series in the same region. The most striking feature of the present volume is its marvelous detail. Exact facts are presented as to the distribution of all of the higher plants, and many of the lower plants. An opportunity is thus given for drawing conclusions as to distribution with almost mathematical certainty. After the usual presentation of historical and geological data, a detailed account is made of the thirty formations of the Hercynic region, placed in ten groups. The body of the work is taken up with a minute discussion of the fifteen subdivisions, into which Drude splits this area. It is here that the individuality and value of this work is best realized; one may well admire the spirit which has prompted the years of exact and careful study making such a volume possible. The closing section treats the relation between the Hercynic and neighboring floras, and the glacial and postglacial history of the Hercynic flora. Not only an abundance of glacial relicts but some interglacial relicts are reported. While the book is scarcely one to be read by one who is unfamiliar with the region, it must be of unspeakable value to German plant geographers. Moreover, all will welcome a volume upon which so much care and pains have been taken to secure an accurate presentation of floristic data.—H. C. COWLES.

MINOR NOTICES.

THREE ADDITIONAL NUMBERS of Karsten and Schenck's *Vegetationsbilder*[7] have recently appeared. Schenck has prepared the third number, dealing with economic plants from the tropics: Thea, Theobroma, Coffea, Myristica, and Carica. The fourth number by Karsten portrays the tropical and subtropical rainy forests of Mexico. The fifth number is issued by Schenck, and consists of pictures from southwestern Africa; a desert with Welwitschia, a euphorbia steppe, a shrub steppe, *Aloe dichotoma*, acacias along a dry stream bed, Euclea. As stated in the former review,[8] these illustrations are accompanied by full descriptions, and set forth most admirably the vegetation features of far distant lands.—H. C. COWLES.

NOTES FOR STUDENTS.

PAMPALONI[9] records two species of fungi from the middle Miocene of Sicily, referring them to the genera *Uncinulites* and *Erysiphites*. They are reconsidered by Salmon,[10] the well known authority on these plants, who considers that *Erysiphites* is not related to the modern Erysiphaceae and that *Uncinulites* should be considered as a species of *Cercosporites*.—E. W. BERRY.

[6] See BOT. GAZ. 35:293. 1903.

[7] KARSTEN, G., and SCHENCK, H., Vegetationsbilder. Hefts 3, 4, 5. *pls. 13–30.* Jena: Gustav Fischer. 1903.

[8] BOT. GAZ. 35:294. 1903.

[9] PAMPALONI, L., Rendiconti della R. Accad. dei Lincei 11: 250–251. 1902.

[10] SALMON, E. S., Journ. Botany 41: 127–130. 1903.

BECK has given us his views respecting the delimitation of plant formations.[11] He discusses the varied use of the term formation, the relations between floristic and biological conceptions, and other disputed questions. Beck believes that true formations are rather sharply marked, and that many "transitions" are developmental stages or are due to man's influence.—H. C. COWLES.

C. C. ADAMS[12] has discussed in an interesting manner the postglacial origin and migration of the life of the northeastern United States. It is shown, especially from his studies of shells, that the southeastern United States is the greatest of the life centers; the southwest has been a secondary center. The Mississippi valley and the coastal plain have been prominent paths of migration.—H. C. COWLES.

R. E. B. MCKENNEY[13] has published some notes on plant distribution in Orange county, southern California. He describes seven formations; the mountains with hard-leaved evergreen shrubs; the foothills, also dominated by a scrubby growth; the cañons, which alone have trees, the river beds, mesas, bogs, and strand. He regards this flora as not properly sclerophyll, but intermediate between this type and the desert.—H. C. COWLES.

MÖLLER,[14] a pupil of Nathorst, has published a flora of the Upper Jurrassic of Bornholm. Contrasted with more southerly localities in Europe, it is distinguished by the presence of a member of the Marattiaceae which at that time are no longer represented to the southward. Several members of the Dipteridinae are also recorded. The Matonieae are represented by specimens scarcely distinguishable from the existing *Matonia pectinata*. Numerous Cycadean leaves are present as are also members of the Ginkgoales.—E. W. BERRY.

J. W. BLANKINSHIP[15] gives a list of the plant formations of eastern Massachusetts with their character plants. His classification is as follows: Xerophytes (sand barrens, hilltop barrens), Mesophytes (sand plain forests, hilly upland forests), Hygrophytes (sand pond margins, low meadows, seashores, low woodlands), Helophytes (swamps, bogs, salt marshes, boggy woodlands), Hydrophytes (sand ponds, mud ponds, sea shoals, fresh-water formations, pelagic formations), Biophytes (waste lands, economic formations, fungoid formations).—H. C. COWLES.

[11] BECK, VON MANNAGETTA, G. RITTER, Ueber die Umgrenzung der Pflanzenformationen. Oesterr. Bot. Zeit. 52: 421–427. 1902.

[12] Jour. Geog. 1: 303–310; 352–357. 1902.

[13] MCKENNEY, R. E. B., Notes on plant distribution in southern California. U. S. A. Beihefte Bot. Centralbl. 10: 166–178. 1901.

[14] MÖLLER, HJALMAR, Bidrag till Bernholms fossile Flora, Kongl. Fysiog. Sällsk. Handl. Lund 13: ——. 1902.

[15] BLANKINSHIP, J. W., The plant formations of eastern Massachusetts. Rhodora 5: 124–137. 1903.

RAUNKIÆR announces[16] that the dandelions in Denmark are parthenogenetic. He finds varations in the common species, on which he bases five new species, besides recognizing two others previously segregated. All these produce fruit freely without fertilization, and even when the flowers of an unopened head are so far sliced off that no stigmas or anthers remain. *Taraxacum obovatum* (Willd.) DC. of southern Europe, *T. glaucanthum* (Ledeb.) DC. from Pamir, and *T. croceum* Dahls, from Greenland and Norway produced fruit without fecundation. Though the author made no cytological study of the case, he searched in vain for germinating pollen or pollen tubes.—C. R. B.

DR. WILLIAM G. SMITH, who has taken up the work of the late Robert Smith,[17] has published the first of a projected series of papers on the distribution of British plants,[18] entitled "Geographical distribution of vegetation in Yorkshire." The methods of Flahault, as applied in Scotland by Robert Smith, have here been employed for the first time in England, and with high success. A map, worked out in extreme detail, forms the basis for the discussion in the text. The moorlands form the most natural vegetation of the district, and are developed as moss moors with much cotton grass, or heather moors with Calluna. The woodlands are dominated by oaks. Much the greater part of the area is cultivated or otherwise modified by man. Nine photographic reproductions of plant associations are inserted in the text. In this connection it may be noted that Dr. Smith has given us an admirable critical review of Graebner's recent studies on the North German heath, comparing the conditions of heath development in Germany and England.[19] —H. C. COWLES.

CASES OF regeneration in the strict sense are of such rarity or of such dubious character among plants as to lead to controversy whether it occurs at all. Pischinger[20] has noted two instances of regeneration in *Streptocarpus Wendlandi* Damm. (Gesneriaceae) which must be conceded to be of the same type as that found in animals. This remarkable plant normally produces no distinct epicotyl and no foliage leaves, but a meristem region develops near the base of the larger cotyledon, which then grows to a foliar structure about 40×20^{cm}. From near the base of this structure arises the scape bearing the inflorescence. In a series of experiments in which a part or all of this leaf-like organ was removed, the entire structure was in two instances regenerated at the surface from which the original had been cut.

[16] RAUNKIÆR, C., Kimdannelse uden Befrugtning hos Mælkebötte. Bot. Tidsskrift **25**: 109–140. 1903.

[17] See BOT. GAZ. **31**: 136. 1901.

[18] SMITH, W. G., Geog. Jour. **21**: 375–401. 1903.

[19] Scot. Geog. Mag. **18**: 587–597. 1902.

[20] PISCHINGER, FERDINAND, Ueber Bau und Regeneration des Assimilationsapparates von Streptocarpus und Monophyllaea. Sitz. Ber. Wiener Acad. **111**: 278–302. *pls. 2*. 1902.

In many cases the "leaf" was regenerated when only a part was removed, but this differs from strict regeneration in that it is development of an organ from an already existent meristem. Studies upon other species of Streptocarpus and upon the nearly related Monophyllaea, which normally produce true foliage leaves, showed many instances of this kind of "regeneration," as well as numerous cases of regeneration in the wider sense of correlated development of other structures.—G. H. SHULL.

THE FIRST account of nuclear conditions in the sexual organs of the Gymnoasceae is presented[21] by Miss E. Dale, who has studied especially *Gymnoascus Reesii* and *G. candidus* (*Arachniotus candidus*). Miss Dale establishes beyond question the presence of a sexual process, supporting in the main the earliest account of this group by Baranetzky in 1872, and discrediting the later views of van Tieghem, Zukal, and Brefeld, who have denied the existence of sexuality.

The sexual organs of *Gymnoascus Reesii* arise as two lateral branches on each side of a septum. They grow out at right angles to the parent hypha and twist around each other, their free ends becoming swollen and finally cut off by a cross wall from the stalks below. These two cells generally fuse while there is yet little differentiation between them, but soon one develops a process that coils around the other, which remains straight and finally becomes spherical. The coiled cell divides by cross walls and from most of the segments one or two short thick branches arise as ascogenous hyphae whose ends develop into asci.

Both sexual cells at the time of fusion contain large numbers of nuclei, and are therefore coenogametes, but when first formed there is only one nucleus in each cell. This nucleus probably divides to give the later multinucleate condition, but Miss Dale did not follow this process, nor did she determine with certainty whether the nuclei unite in pairs after the fusion of the coenogametes. The nuclei pass into the coiled prolongation, and thence into the ascogenous hyphae. The nuclear history during the development of the ascospores was not studied in detail. In *Gymnoascus candidus* the two coenogametes may not arise from the same hypha or simultaneously as in *G. Reesii*, but otherwise the two forms agree in all essentials.

These studies add another type to the rapidly growing list of lowly Ascomycetes whose sexual organs are coenogametes, and indicate that this condition is likely to prove very general in the group. The possible bearing of this on the problems of the origin and relationships of the Ascomycetes is of great interest in connection with the conditions prevalent in the Mucorales, Saprolegniales, and Peronosporales—a subject which the reviewer has recently considered in his paper on "Oogenesis in Saprolegnia."[22]—B. M. DAVIS.

[21] DALE, ELIZABETH, Observations on Gymnoasceae. Ann. Botany **17**: 571–596. *pls. 27, 28.* 1903.

[22] BOT. GAZ. **35**: 233. 1903.

NEWS.

MR. A. A. HELLER has removed to Los Gatos, California.

DR. JOHN L. SHELDON has been appointed professor of bacteriology in the University of West Virginia.

DR. JOSEPH H. MELLICHAMP, an ardent student of the southern flora, died October 2 in James Island, S. C.

THE ATTENTION of subscribers is directed to the announcement in the advertising pages regarding the general index. The error in the first notice is corrected, and we hope the approval of the index will be general enough to insure its publication by the University Press. It is already in an advanced stage of preparation.

MR. CORNELIUS VAN BRUNT, an expert photographer of native plants, died at his home in New York city on October 1, at the age of seventy-seven. No one who once had the pleasure of seeing the wonderful lantern slides made by Mr. Van Brunt, and colored to the life by Mrs. Van Brunt, will ever forget the perfection of their technical skill, directed as it was by their keen appreciation of floral beauty.

THE SEVENTH annual meeting of the Society for Plant Morphology and Physiology will be held at Philadelphia, Pa., in conjunction with the meetings of several other scientific societies, on December 29, 30, 31, 1903. This is the first meeting of this society in Philadelphia, though the preliminary steps which led to its formation were taken there at the meeting of the American Society of Naturalists in December 1895.

MR. A. M. FERGUSON, instructor in botany in the University of Texas, has been given leave of absence for one year by the University of Texas, and has been appointed special agent for the office of Pathology and Physiology, Bureau of Plant Industry, to investigate technical problems in connection with mushroom culture. He has been assigned to the botanical department of the University of Missouri. He has been recently occupied with the study of the so-called fungus gardens of the various species of fungus-eating ants occurring in Texas.

PROFESSOR B. E. FERNOW, late director of the New York State College of Forestry, is writing a book on biological dendrology. He is also giving privately courses on Forest management and Forest finance to a number of former students of the College of Forestry, who have returned to Cornell University for a baccalaureate degree and to finish their forestry education by

means of these courses. Most of the Junior students of the abandoned college have gone to the Forest School at Yale University. The *Forestry Quarterly* will be continued by Mr. Fernow.

THE BOTANICAL SOCIETY OF AMERICA will hold its tenth annual meeting at St. Louis December 29–31, 1903, under the presidency of Professor C. R. Barnes, of the University of Chicago. Headquarters will be established at the Southern Hotel, and sessions will be held in the Central High School. The retiring president, Dr. B. T. Galloway, chief of the Bureau of Plant Industry, will deliver an address upon *What the twentieth century demands of botany*. Mr. Francis Darwin, of the University of Cambridge, will present a paper upon *A self-recording method applied to the movement of stomata.*

IN CONNECTION with the International Botanical Congress to be held in Vienna about the middle of June 1905, it is proposed to hold a botanical exhibition. The International Association of Botanists desires to demonstrate the importance of its proposed central bureau by exhibiting material to illustrate its functions. These functions have been defined as follows: "(1) To give information as to the places where certain collections, herbaria, etc., can be consulted; as to cost of living at places likely to be visited by botanists; as to botanical expeditions in preparation, etc. (2) To form a library of separate reprints of botanical papers which can be loaned to members who so desire, subject to the payment of postage both ways. (3) To form a center for the exchange, sale, and purchase of photographs of plant-societies, plants, or parts of plants. (4) To obtain and distribute material for investigation. (5) To assist in exchanging or selling microtome-sections. (6) To aid in obtaining and distributing demonstration material. (7) To be a center for obtaining, keeping alive, and distributing pure cultures of algae and fungi." It is especially desired that a complete collection of reprints of every author may be obtained for this exhibition with a view of presenting these to the library of the central bureau. All material intended for this exhibition is to be sent before May 1, 1905, A. d. Botanischen Garten der K. K. Universität in Wien, III, Rennweg 14. The cost of transportation is to be borne by the person exhibiting. Further information may be obtained from Mr. J. P. Lotsy, 33a Oude Rijn, Leiden, Holland.

VOLUME XXXVI NUMBER 6

BOTANICAL GAZETTE

DECEMBER, 1903

ON THE GEOGRAPHIC DISTRIBUTION AND ECOLOGICAL RELATIONS OF THE BOG PLANT SOCIETIES OF NORTHERN NORTH AMERICA.

EDGAR N. TRANSEAU.

(WITH THREE MAPS)

BY the term "bog-plant societies," as used in this paper is meant that group of plant societies which is commonly found inhabiting undrained depressions and marshy grounds in the northern United States and Canada. In the northern states they have become noted for their possession of such anomalous plants as the sundew, pitcher-plant, tamarack, and cranberry. Although not so well known, the cassandra, rosemary, and Labrador tea are quite as interesting.

"DRAINED SWAMP" AND "UNDRAINED SWAMP" SOCIETIES.

There have been a number of descriptions of these bogs published in connection with local ecological studies, and in several instances have comparisons been made between them and the other swamps of the region. They are referred to as "undrained swamps," in contrast with the groups of "drained swamp" societies which may be found on adjoining low grounds and along stream courses. The latter group may be briefly summarized by noting that in the region under discussion it is commonly made up of such plants as Typha latifolia[1], Scirpus lacustris, Juncus effusus, Carex riparia, Polygonum emersum, P. sagittatum, Cephalanthus occidentalis, Cornus stolonifera, C. candidissima,

[1] Nomenclature of Britton's Manual of the Flora of the Northern States and Canada, 1901.

Salix discolor, Acer rubrum, Ulmus americana, and Fraxinus americana.

While it often happens that locally the one occurs only in drained conditions and the other only in undrained situations, field work carried on over any considerable area will show that drainage conditions are not adequate to account for the presence or absence of either of these two distinct types of vegetation. The presence of peat, with the consequent accumulation of humus acids, has been commonly spoken of as preventing the coming in of the "drained swamp" types. In southern Michigan and northern Indiana, however, there are many swamps with a thick substratum of peat and without an outlet, yet supporting a vegetation made up wholly or in part of these plants. It is true, however, that the bog societies occur here only in poorly drained situations, underlaid with peat or bogus soil.

Again, it is not unusual to find these two society groups growing on opposite sides of the same lake, where the underlying soil can be shown to be the same. To account for this, it has been suggested that the depth of water in the two situations is of importance. But any ideas of this kind can be disproved by carrying the criteria into a new locality. Just to the west of Ann Arbor, Mich., occurs a small glacial lake. This was formerly surrounded by a quite typical group of bog societies. Within recent years the eastern side of the lake has been entirely cleared, and a large part of the original tamaracks on the south and southwest sides have been cut away. There is left a rather pure growth of bog plants on the northwest side. Since the clearing was made on the southwest side there has sprung up a dense growth of herbs, shrubs, and trees, nearly equaling in height the adjoining grove of tamaracks. But if we note the species prevailing in this area, we find the plants enumerated above as typical of drained swamps. It is practically impossible to account for this situation on the basis of soil difference, chemical character of the soil solution, drainage conditions, or depth of water.

In his paper on the "Physiographic Ecology of Chicago and Vicinity" Cowles[2] distinguishes one "drained" and three

[2] BOT. GAZ. 31:145–155.

"undrained" types of swamps occurring in the area of lakes and sand dunes at the southern end of Lake Michigan. Although several species of plants may be common to two or more, he does not believe these societies to be related to one another genetically.

That a certain amount of chance in the matter of seed dispersal must be taken into account in any botanical field problem is recognized. But the fact that "drained" and "undrained" swamps occur in close proximity to one another, each with numerous examples in the same district, seems to require some more adequate explanation.

RELATION TO SURROUNDING VEGETATION.

Throughout the region of northern Indiana, northern Ohio, and southern Michigan the problem is still further complicated by a seeming absence of all connection between the bog societies and the bordering forests. The zonal succession of plant groups, from the submerged aquatics of the pond to the arborescent forms of the higher bog margin, are clearly defined and well known. But then comes a sudden break, and without a suggestion of gradation the surrounding forest of mature oaks or oaks and hickories appears.

Farther north in Michigan there is no such difficulty in finding a definite order of succession between the bogs and forests surrounding them. For example, a tamarack swamp on north Manitou Island, which is surrounded by a thick forest of maple and beech, shows the following societies arranged almost zonally, beginning with the open pond in the center:

1. AQUATIC SOCIETY. Potamogeton natans, P. lucens, Nymphaea advena, Castalia odorata.

2. CAT-TAIL-DULICHIUM SOCIETY. Typha latifolia, Phragmites Phragmites, Menyanthes trifoliata, Dulichium arundinaceum, Cicuta bulbifera, Scheuchzeria palustris.

3. CASSANDRA SOCIETY. Chamaedaphne calyculata, Dryopteris Thelypteris, Sphagnum sp. ?, Kalmia glauca, Sarracenia purpurea, Ledum groenlandicum, Lycopus americanus, Triadenum virginicum, Polygonum Hydropiper, Rubus hispidus, Comarum palustre, Andromeda Polifolia, Chiogenes hispidula, Oxycoccus Oxycoccus, and Eriophorum virginicum.

4. SHRUB AND YOUNG TREE SOCIETY. Aronia arbutifolia, Ilicioides mucronata, Rosa caroliniana, Ilex verticillata; young specimens of Larix laricina, Betula pumila, Picea Mariana, and Acer rubrum. Beneath these occur a scattering of members of the preceding society, together with Limnorchis hyperborea, Blephariglottis lacera, Gymnandeniopsis clavellata, Osmunda regalis, O. cinnamomea, Dryopteris spinulosa intermedia, Vaccinium canadense, Epilobium lineare, E. adenocaulon, and Viola blanda.

5. CONIFER SOCIETY. This zone is composed of mature tamaracks, black spruces, low birch, and swamp maples; young and mature Betula lutea and Tsuga canadensis; and seeding Acer saccharum. The undergrowth of herbs and shrubs is diminished to a few stragglers. This brings us to the higher ground surrounding the bog, which is occupied by the next society.

6. CLIMAX FOREST SOCIETY. Consists of sugar maples and beech trees with occasional hemlocks. The undergrowth is sparse, consisting principally of their own seedlings.[3]

Going farther north into Ontario, the series of societies is not so long, but apparently just as definite. But we have there passed the northern limits of our broad-leaved mesophytic trees and the climax stage is reached in a mixed forest of pine, spruce, and fir. This same statement probably holds for the great coniferous areas of Wisconsin, Minnesota, New York, northern Pennsylvania, and the New England states. Even so far south as northern Indiana, in the sand-dune region, Cowles[4] has shown that where the surrounding vegetation consists of pines there is no doubt the same order of succession.

It appears then that where the northern conifers are dominant or make up an integral part of the forests, the ecological relations of the bog societies are clear. In other words, they normally represent one physiographic starting-point for the development of the great conifer forest formation.

There remain therefore at least two questions to be solved:

[3] See also WHITFORD, H. N., The genetic development of the forests of northern Michigan. BOT. GAZ. 31:315. 1901.

[4] *Loc. cit.*, p. 150.

First. What relation do these bog societies bear to the surrounding vegetation of oaks and hickories as they occur in Ohio, Indiana, and southern Michigan?

Second. How can we account for the presence of bog societies and swamp societies (or mixtures of the two) when found in adjacent areas, having similar drainage and soil conditions?

PRESENT DISTRIBUTION OF BOG PLANTS.

In order to obtain a better understanding of these questions, data on the geographic distribution of bog plants were collected and maps drawn. It soon became evident that the number of species would have to be limited and that only those which are characteristic of these situations across northern North America could be considered. The number was finally reduced to fifteen. Beginning with those which first find a foothold in such depressions and continuing in their approximate order of advent, they are: Menyanthes trifoliata, Dulichium arundinaceum, Comarum palustre, Scheuchzeria palustris, Eriophorum polystachyon, Drosera rotundifolia, Sarracenia purpurea, Oxycoccus Oxycoccus, Chiogenes hispidula, Andromeda Polifolia, Chamaedaphne calyculata, Ledum groenlandicum, Kalmia glauca, Betula pumila, and Larix laricina.

Finally the accompanying map (*fig. 1*) was drawn by superimposing the areas of North America in which each of these plants commonly occurs. In the course of its construction some interesting points in geographic distribution came to light. The dark area extending from the Atlantic to the Mackenzie basin represents a great center throughout which all these plants appear in most bogs. The lighter shaded areas north and south represent territory in which only a majority of the forms occur in the average bog, while in the lightest shaded portions only a minority of them are to be found.

CLIMATE OF THE OPTIMUM REGION.

The region of optimum distribution is limited by certain climatic barriers. On the southwest its limits coincide closely with those of the forests. Beyond this area the relation between rainfall and evaporation makes the conservation of water in

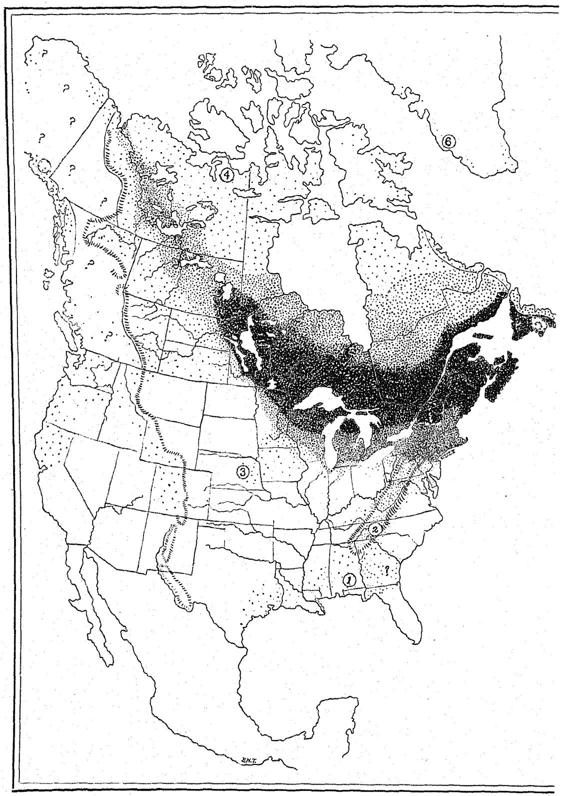


FIG. 1.—Map showing distribution of bog plants. (1) Drosera, Dulichium. (2) Sarracenia, Drosera, Dulichium, Eriophorum, Chiogenes, Chamaedaphne. (3) Dulichium, Menyanthes. (4) Drosera, Comarum, Menyanthes, Eriophorum, Ledum, Andromeda. (5) Drosera, Comarum, Menyanthes, Eriophorum, Oxycoccus, Andromeda, Ledum, Kalmia, Chamaedaphne. (6) Menyanthes, Oxycoccus, Ledum, Andromeda, Kalmia. The presence of a large number of shrubs in Alaska and Greenland is probably connected with their preservation there during glacial times.

depressions throughout the year impossible. On the south and southeast, while the rainfall and relative humidity are favorable, the intense insolation of the summer months seems to be the controlling factor. The northern boundary coincides with that of the northern limits of dense forests. According to Kjellman,[5] Kihlman[6] and Warming,[7] this boundary is controlled by the amount of snowfall, exposure to dry winter winds, and the length of the growing season. There does not appear to be any relation between the distribution of this group of plant societies and the "life zones" distinguished by Merriam.[8] Within the belt of optimum conditions the climate is characterized by great range of temperature, both daily and annual. As we go toward the east from the Mackenzie basin, this is modified by the increase in relative humidity. The summers are short, bright, and warm, with abundant rainfall, principally in the form of thunder showers. The winters are long, and extremely low temperatures may occur. The snowfall increases from a foot or two in the western part to several feet in Ontario and the St. Lawrence basin. In the Northwest Territories, where the tundra vegetation is dominant, the ground below a depth of a few centimeters is frozen practically throughout the year. Since air temperatures of 21° C. are common in late spring and summer, the plant roots and shoots must there withstand remarkable temperature differences. With the exception of the eastern maritime provinces and Maine, no part of this optimum area is comparable with the conditions which call forth the great bog development of northern Germany and Scandinavia. In the latter localities the bogs are confined to depressions, but may occur in a variety of topographic situations. They may even invade established forests, and by raising the ground water level destroy the tree covering.[9]

[5] KJELLMAN, F. K., Aus dem Leben der Polarpflanzen. Leipzig. 1883.

[6] KIHLMAN, A. O., Pflanzenbiologische Studien aus Russisch-Lappland. Acta Soc. pro Fauna et Flora Fennica 6. 1890.

[7] WARMING, E., Ueber Grönlands Vegetation. Engler's Botan. Jahrbücher 10. 1888.

[8] MERRIAM, C. H., Life zones and crop zones of the United States. Bull. 10, U. S. Dept. Agric. 1898.

[9] GANONG, W. F., Raised peat bogs in the province of New Brunswick. Proc. Roy. Soc. Can. II. 3^4: 131–163. 1897.

It is also worthy of note that in the southeastern part of this region the bog flora is increased in variety by a large number of plants whose range is more southerly than that of the typical bog plants. Among these are Vaccinum corymbosum, V. atrococcum, Rhodora canadensis, Aronia arbutifolia, and Viburnum cassinoides. Their distribution points to a northward migration from the southern Appalachians.[10]

VARIATIONS OF THE BOG FLORA IN GEOGRAPHIC RANGE.

But the map has a still greater significance. The dark area represents the region in which most of these plants attain their highest physical development. Those who have seen the magnificent groves of tamarack in the north, attaining a height of thirty meters and a bole diameter of a meter, will appreciate this fact when they compare them with the stunted groups of the larch in the bogs near the southern and northern limits.

Again, within this same belt, at least eight of the plants, the buckbean, cranberry, snowberry, rosemary, leather leaf, labrador tea, birch, and tamarack, are not confined to bog areas. They may be said to have there a wider life-range and are to be found in a variety of habitats. The tamarack, for example, is found on the hills and along most of the streams. With the black and and white spruce and pine, it makes up a large part of the forest. Here too the buckbean, leather leaf, Labrador tea, and birch occur along slow streams, and the rosemary, snowberry, and cranberry in moist ravines and rich woods.

Just as striking, perhaps, is the fact that as we go in any direction away from this optimum region, the first plants to diminish in size and frequency of occurrence are the arborescent tamarack and birch. Then follow in close succession the shrubby forms, and finally the herbaceous species.[11] This is practically a reversal of the order of their coming into a new area, and, as we shall see later on, this may have some connection with the

[10] ADAMS, C. C., Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. 3:123. 1903.

[11] *Scheuchzeria palustris* is an exception, so far as its eastern distribution is concerned, and has about the same range as *Betula pumila*, but in the west it reaches its southern limit in Colorado and California.

migration this vast aggregate of bog societies has made since the glacial period. It also represents an order from the tallest forms to those raised but slightly above the wet substratum.

PREGLACIAL DISTRIBUTION.

Of these fifteen species, three, Dulichium, Sarracenia, and Kalmia, are endemic. The larch and birch are represented in the Old World by closely related forms, while the remaining ten occur in similar habitats in Europe and Asia. This naturally points to their origin, and certainly indicates their preglacial distribution to have been in the circumpolar regions of both continents. It also implies that these great land masses must have been connected for a long time during the Tertiary period, so that migration from one to the other was by no means difficult. Whether these forms originated in a single polar area is of little consequence. They may have arisen partly in America, partly in Eurasia, but they were essentially the products of similar conditions and by migration came to be associated.

THE GLACIAL MIGRATIONS.

With the coming on of the cold period, which closed the Tertiary and inaugurated such extremes of climate between the equator and the poles, the consequent accumulation of ice on these northern continents destroyed the ancient habits of these plant societies. At the same time semitropical species, which were common alike to high and low latitudes, were killed by the increasing cold, the ground they had covered affording new areas for occupancy. By the reversal of the drainage lines and consequent destruction of low-ground vegetation, new habitats suited to these plants arose in advance of the ice invasion. Just as the zones of vegetation in a small lake move toward the center, because that is the only direction in which development is possible, so these plants spread away from the centers of ice accumulation. Where this migration moved to the west the plants were later on destroyed, but their southward extension brought them into areas which were not within reach of the subsequent ice invasion. Their adaptations for rapid seed dispersal are not

notable, except in the case of the Dulichium and cottongrass. The larch and birch have winged seeds, while the remainder would seem to be dependent upon transportation by birds and water currents. But the fact that the plants have survived the ice advances proves that they were easily able to establish themselves in new areas as rapidly as the climate changed. Not less than five such geographic migrations of more or less latitude, corresponding with the five glacial epochs, must have occurred. Between them were intervals when the temperature, as shown by plant and animal remains[12] found in interglacial deposits, was fully as high as at the present time. If we consider this proved, then the only glaciation which could materially affect the distribution of our boreal societies today is that of the last or Wisconsin epoch. Through the work of Chamberlin,[13] Leverett,[14] Salisbury,[15] Upham,[16] and others, the limits of this ice invasion have been definitely mapped.

In order to get an idea of the distribution of the boreal plant societies during the maximum glaciation, let us try to picture what would become of these same societies if a similar period of glaciation were to come upon them now. A sufficient time has probably intervened since the last glacial epoch to allow of almost perfect climatic adjustment on the part of the tundra and conifer societies, so that the climate now most favorable for their development may well have characterized a zone just beyond the ice margin. This zone would gradually move with the increase of the ice fields until it would come to occupy the position shown in *fig. 2*. According to Chamberlin, the climatic conditions pre-

[12] COLEMAN, A. P., Glacial and interglacial beds near Toronto, Jour. Geol. 9: 285. 1901. PENHALLOW, D. P., The Pleistocene flora of the Don Valley. Rept. Brit. Ass. Adv. Sci. 1900: 334.

[13] CHAMBERLIN, T. C., Classification of American glacial deposits. Jour. Geol. 8: 270; The glacial phenomena of North America, Geikie's *Ice Age*, 3d ed. p. 274. 1894.

[14] LEVERETT, F., Changes of climate indicated by interglacial beds. Proc. Bost. Soc. Nat. Hist. 24: 455. 1890.—The Illinois glacial lobe. Mon. 38, U. S. G. S.—The glacial formations and drainage features of the Erie and Ohio Basins. Mon. 41, U. S. G. S.

[15] SALISBURY, R. D., and ATWOOD, W. W., The geography of the region about Devils Lake and the Dalles of the Wisconsin. Bull. 5, Wis. Geol. and Nat. Hist. Sur. SALISBURY, R. D., Glacial geology of New Jersey. Rep. State Geologist N. J. 5. 1902.

[16] UPHAM, W., The Glacial Lake Agassiz. Mon. 25. U. S. G. S. 1896.

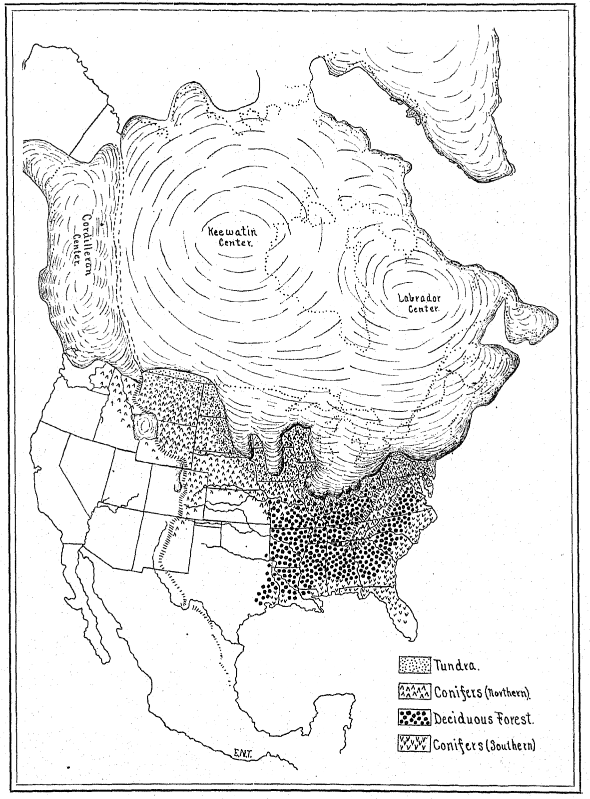


FIG. 2.—Map showing hypothetical distribution of forests and tundra during maximum glaciation of the Wisconsin Epoch.

vailing about the margin were intermediate between those of Greenland and Alaska at the present time. In the former case the vegetation is sparse and of tundra type, in the latter the forests occur on the stagnant ice margin.[17] It would appear then that the glaciers would not affect the tree distribution at any great distance from the ice front. But there are other factors which would affect the breadth of the zone of conifer dominance. As we may learn from their present distribution, a dry climate, a youthful topography in which erosion is active, high elevation and sterile soil, all of which imply great variations in temperature and relative humidity, are more favorable to conifers than to broad-leaved deciduous trees.

It should also be noted in connection with the development of the continental glacier that, as the ice sheets spread from the two great centers of accumulation, they unite in the region north of lakes Superior and Huron. With their near approach to the lakes, the area of conifers is divided into an eastern and western section. As the development proceeds toward the Wisconsin terminal moraine, the western section would be forced toward the Great Plains, while the eastern division would spread south to the Appalachian highlands and coastal plain.

But in the interior the Ohio basin was occupied by the oaks, ash, hickories, elms and maples. Judging by the present northern limits[18] of some of these species it is doubtful if the conifers could compete with them at any great distance from the ice front, so that the belt of tundra and conifers may have extended as far south as the Ohio; but it seems probable that even north of this river species of oak, ash elm, and maple persisted.

DISTRIBUTION DURING MAXIMUM GLACIATION.

To be more definite, let us briefly note the conditions that would prevail during the time of maximum extension, from the Atlantic to the Rockies. In New Jersey, with its extensive area of sand and slow-flowing streams, conditions must have been

[17] RUSSELL, I. C., Glaciers of North America. Ginn & Co. 1901.

[18] BELL, R., The geographical distribution of forest trees in Canada. Scot. Geog. Mag. 13:281. 1897.

favorable for a wide-spreading zone of boreal societies. In Pennsylvania the high relief of the Appalachians and consequent low temperature also afforded exceptional opportunities for the spread of these societies far to the south. Here too the cold water of the glacial drainage pouring down the numerous tributaries of the Allegheny, Susquehanna, and Delaware rivers may have had a marked influence by lowering the temperatures of the narrow valleys, just as the streams which flow from Mount Katahdin and the glaciers of Mount Hood (Cowles) and Mount Shasta (Merriam)[19] affect the temperature of their adjacent valleys today. The presence of many such northern forms as the white pine, spruce, and hemlock in areas of the southern Appalachians has long been attributed to the glacial period.[20] In the Ohio valley the streams flowing from the south would aid in maintaining equable temperatures and preserving the broad-leaved mesophytes as far north as the Ohio River. Beyond the Mississippi the conditions must have resembled those now prevalent in the Saskatchewan basin. Bessey[21] reports the occurrence in Nebraska of deposits of "well defined branches, twigs and occasionally tree trunks" at depths varying from twenty to fifty feet below the surface, and concludes that in recent geological times there must have been extensive conifer forests throughout the state. The present distribution of trees in Nebraska shows outliers of the western yellow pine (*Pinus ponderosa scopulorum*) in the central part of the state far removed from the main area of its occurrenee.

Now as to the bog plants: since under favorable conditions they may occupy other habitats than undrained depressions, they probably existed on the borders of the heavily loaded streams, in ravines and moist situations generally along the whole ice front. It is to be noted that practically all of the

[19] MERRIAM, C. H., Results of a biological survey of Mt. Shasta, California. North Americana Fauna no. 16. 1899.

[20] GRAY, A., Forest geography and archaeology. Amer. Journ. Sci. and Arts III. 16:85. 1878. HOOKER, J. B., The distribution of North American flora. Amer. Nat. 13:155. 1879.

[21] BESSEY, C. E., The forests and forest trees of Nebraska. Ann. Rep. Neb. State Bd. of Agri. 1888:93.

existing small lake areas of the northern states were covered by the ice during the maximum extension of the Wisconsin ice sheet. As there is no reason to believe that the drift sheets of the preceding epochs, which in many places extend beyond the Wisconsin terminal moraine, contained such small undrained depressions, it follows that the bog societies must have occupied other habitats.

POSTGLACIAL NORTHWARD MIGRATION.

With the renewal of a milder climate and the consequent recession of the glaciers, the plant societies would gradually spread in the direction of continuous habitats and generally northward. The bog and tundra types would be the first to push into the barren ground left by the retreating ice. The area over which they spread in early postglacial times must have been very much more extensive even than that now occupied by them. In the smaller glacial depressions where absence of wave action would favor littoral vegetation, the bog plants would become firmly established. On the western and eastern sides of the glaciated area the tundra would be closely followed by the conifer forests.

In the west the spreading of the conifers to the north was followed by their gradual destruction in the southwest, due to the increase in temperature as compared with the rainfall. It is possible that the rainfall in Nebraska was never any greater than at the present time. But the decrease in transpiration accompanying decrease in temperature might account for the presence there during glacial times of trees which cannot live under present conditions. The bog plants perished with the conifers and their southwestern boundaries today correspond with that of the forest.

In the east, among the highlands, exceptional circumstances were afforded for the preservation of these northern forms. Many relicts still crowd the higher elevations as far south as western North Carolina.

But in the northern Ohio valley, with its scant conifer vegetation, the areas which at that time supported the bog societies

were encompassed by broad-leaved forests. The oaks, hickories, maples, ash, and elm, following the lines of their specific habitat, the stream valleys or uplands, the sandy stretches left by glacial drainage, or the long lines of clay moraines, surrounded them in their northward progression.

Probably if the pines, spruce, and hemlock had ever been dominant in Ohio, Indiana, and southern Michigan we should find some evidences of their former occupation by way of isolated conifer areas. Excepting the southern and eastern shore of Lake Michigan and two small groups of pines in Ingham and Calhoun counties, Michigan, no conifer areas occur south of the Grand and Huron River valleys. When the early settlers moved into the region of southern Michigan, its forests were of the type commonly known as "oak openings." Probably no type of broad-leaved forest would be more favorable for the preservation of conifer areas had they been dominant for any great length of time after the ice retreat. Where they have been planted within this region, they flourish and attain their normal proportions. Judging by the present distribution of *Pinus Strobus* and *Pinus resinosa*, the character of the soil in the vicinity of lakes Michigan, Huron, and Erie, and the meteorological conditions associated with these lakes, it seems probable that the conifers have reached their present distribution in the lower peninsula of Michigan by way of the lake shores. Probably the great bulk came by way of the southern end of Lake Michigan and from Ontario.

In the west, the north, and the east, then, the xerophytic bog societies are still found with their natural associates, the conifers (*fig. 3*). But in the Ohio valley they have been surrounded by a vegetation which bears no direct relation to them. Naturally, therefore, we should not expect to find an order of succession between them. This seems to be the answer to the first question proposed.

RELATION OF BOG SOCIETIES TO THE SWAMP SOCIETIES.

This also gives us a new basis for answering the second question, as to the presence of the bog societies and swamp societies

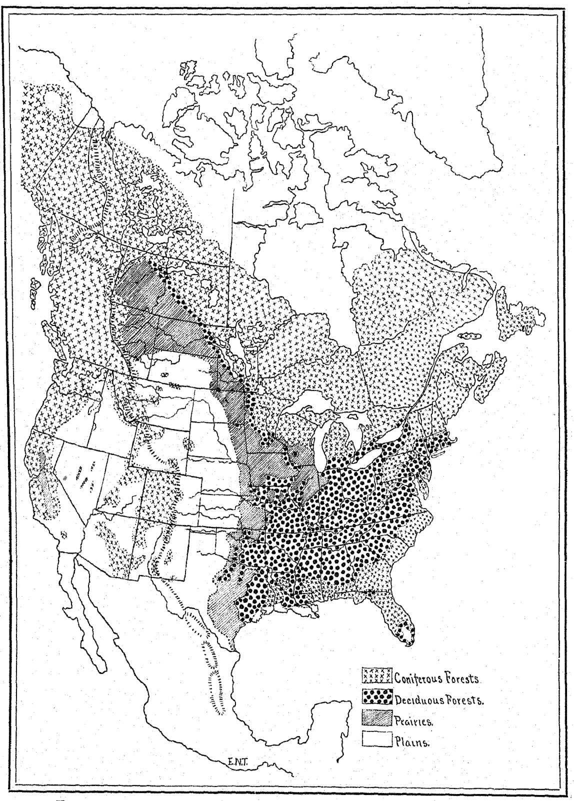


FIG. 3.— Map showing present distribution of forest, prairie and plains. (After Sargent, 10th Census, Vol. 9.)

in adjacent areas. As we know from the numerous physiographic studies that have been made of glacial basins, many of the lakes were formerly much larger than at present. Some of them in early postglacial times had steep banks, which were unfavorable to the development of shore vegetation. But by the lowering of the water level consequent upon the cutting down of the outlet, the shore line at present is a gradually sloping one, and supports a "drained swamp" flora. In other cases irregular arms, extending away from the main body of the lake and protected from wind and wave action, doubtless supported a bog vegetation during the tundra dominance. Since then they have been separated from the main lake by a lowering of the water level. Today we find in many such cases the bog vegetation still persisting in the depressions which were formerly arms of the lake, while on the shore of the main body, which came to be swampy at a much later period, the so-called "drained swamp" flora occurs. One of the best examples of this is Turkey Lake, Indiana. Here is an irregular lake several square miles in extent, nearly surrounded by high moraines. At its southeastern end, through a less elevated portion of the moraine, it formerly connected with several shallow depressions,[22] all of which contain bog plants with varying proportions of swamp plants. But on the now shallow margins of the present lake only the swamp plants are found. At Eagle Lake[23] the same observations hold for a former extension of this lake toward the northwest. But without multiplying examples, the relation of these two groups of swamp societies seems to depend largely upon the time when the swamps came into existence as swamp habitats. If they have existed since the days of tundra conditions they may show a bog flora today. If they are of recent origin, the plants will correspond to the normal swamp plants of the present climatic conditions. If of intermediate age, we may have various mixtures of the two. Dr. Cowles informs me that the only bog in the sand-dune region near Chicago which contains all these typical bog plants is the one that occurs on the Valpa-

[22] For map and description of lake see Proc. Ind. Acad. Sci. 1895.

[23] Map opposite p. 118, Proc. Ind. Acad. Sci. 1901.

raiso moraine. When this basin was formed the area occupied by the other bogs was still covered by the waters of Lake Chicago (now Michigan). At the present time new bog areas are being continually added by the interference of the moving dunes with drainage lines. And these new areas frequently contain a number of the bog plants. This, however, does not invalidate the explanation here suggested. The bog habitat has been continuous since early postglacial times; only its position and extent have been variable.

This same observation holds in the case of certain lakes which have long supported a growth of the bog plants at some part of their shore line. By recent gradual changes of level, or by the development of a floating sedge and cassandra zone, these areas have been greatly enlarged in recent times. Usually, however, such formations are partially made up of swamp species.

It is a well-known fact that in many localities where the bog societies formerly existed, they have partially or entirely disappeared. Since the settlement of this region, extensive bog areas have been cleared and drained. Fires have aided in the destruction of the tamaracks, and in many places the sudden lowering of the water level due to ditching has resulted in the killing of a large part of the original bog flora.

In this connection it is to be noted that the partial clearing or burning of a swamp area opens up a new territory for occupation, either by the bog plants or the swamp plants. The preservation of the underground stems of many of the bog species makes their chances more favorable for capturing the area in question. But there are many areas to the west of Ann Arbor which show that these bog plants cannot compete with the swamp plants in the occupancy of new territory, even though the bog plants be in complete possession previous to the clearing. We may say that the chances of capturing newly exposed land areas at the present time are all in favor of the swamp plants, largely because of their greater production of seeds, more adequate means for seed dispersal and better adaptations to present climatic conditions. In early postglacial times, however, the conditions were far different. The swamp plants had been

driven further south. The climate being more boreal in its character favored the bog plants, so that they became practically the only competitors for the low-ground situations.

The preservation of the bog societies in poorly drained situations down to the present time seems to be due (1) to the lower temperatures prevailing there, (2) to the sterile nature of the substratum, (3) to the completeness with which the substratum is occupied by the bog plants, and (4) to the fact that most bog habitats are associated with lakes, whose basins must be entirely filled with débris, before the drainage conditions will be naturally improved and made more favorable for the coming in of other plant societies.

To account for the xerophytic character of many of the bog plants, experiments now being carried on seem to indicate that differences of temperature between substratum and air is adequate. But the presence in many of our bog habitats of swamp species which show no xerophytic adaptations suggests that such xerophytic structures may be unnecessary under present conditions in *this* region.

SUMMARY.

To summarize the results of this study, we may say that, as shown by their geographic distribution:

1. The bog societies are typical of the colder portions of North America and are closely related to the bog societies of Europe and Asia.

2. They show an optimum region of dispersal having a moist climate, subject to very great temperature extremes. Within this region the plants have a greater range of habitats and an increased physical development.

3. As we go away from this center, either north or south, the first forms to show the effect of climatic change in diminished size and frequency of occurrence are the arborescent species. The species which extend furthest from this optimum region are herbaceous forms.

4. The bog societies are normally related to the conifer forests in their development to a climax tree vegetation.

5. Where surrounded by oaks and hickories, or in general

when conifers are absent, they show no order of succession to the forest societies. This is to be explained on the basis of the migrations forced upon all boreal societies during glacial times.

6. The absence of conifers in the Ohio basin probably indicates the dominance of broad-leaved forms there during glacial times.

Local lake and bog studies seem to indicate that:

1. Present bog habitats are continuations of similar habitats which existed in early postglacial times, when tundra conditions and tundra vegetation were dominant.

2. The temperature phenomena of undrained depressions, containing deposits of peat, are favorable to the preservation of these types.

3. The "drained swamp" and "undrained swamp" classification will not hold over any great area. Undrained and drained depressions are both favorable to the development of the common swamp plants.

4. The bog societies are composed of boreal species and, in so far as the area of Ohio, Indiana, and southern Michigan is concerned, must be considered as relicts of former climatic conditions. The swamp societies, made up of more southerly forms, must be considered as the normal hydrophytic vegetation of the present climatic conditions.

The above results are put forth preliminary to a more detailed account to be published later. It is hoped that by this publication the author may be enabled to secure further data as to bog societies in other localities.

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ARALIA IN AMERICAN PALEOBOTANY.

EDWARD W. BERRY.

IN a study of the mid-Cretaceous floras of the Atlantic coastal plain, the difficulty of determining by what characters certain leaves were allied to Aralia, Sassafras, or Sterculia led to a somewhat extended review of these genera, more particularly the former, which is so abundantly represented throughout the American Cretaceous and Tertiary.

As to the relationship of these leaves with modern species of Aralia, we are not here especially concerned. Leaves of this type, however, are such a constant feature of these ancient floras, both in this country and abroad, that they possess an unusual degree of interest, and I have endeavored in the following notes to define more precisely the characters which serve to distinguish these leaves from leaves of other genera with which they are often confused.

The existing species of Araliaceae number about 450, which Harms, in *Die natürlichen Pflanzenfamilien*, distributes among 51 genera. They are widely distributed in the temperate and tropical regions throughout the world, and include herbs, shrubs, and trees with simple, lobed, or compound leaves. The genus Aralia, as restricted, includes some 27 species of North America and Asia with ternately and pinnately decompound leaves. The only fossil form which seems to stand in this ancestral line is *Aralia triloba* Newb. from the Fort Union Tertiary.

In North America north of Mexico we have six existing species of Aralia, four eastern and two western (besides three varieties). Of these *Aralia spinosa* L. is the only arborescent form. Beside Aralia two other genera occur with us: Panax, with two eastern North American species and five species of central and eastern Asia; and Echinopanax, with one species on the Pacific coast of America, which reappears in Japan. Many other genera occur in the West Indies, Mexico, Central and South America.

The fossil species throughout the world have mostly been referred to Aralia or Hedera, and are comparable for the most part with the existing species of the Araliaceae as a whole, rather than with these respective genera. Beside these two genera, various fruits from the Atane and Patoot beds of Greenland, and from the Miocene of Europe, have been referred to Panax; Unger identifies a species of Cussonia from the Miocene (Kumi) of Greece, Velenvosky another from the Cenomanian of Bohemia, and Nathorst a species of Acanthopanax from the Pliocene of Japan. Some 44 species of Aralia leaves have been identified from American strata, ranging from the Potomac formation upward through the Miocene. Numerous analogues of these American species have been described in Europe, as well as five species which are identical. Thus *Aralia coriacea* Velen., occurs in the Cenomanian of Bohemia and at Marthas Vineyard; *Aralia transversinervia* Sap. & Mar. occurs at Gelinden and has been reported from Long Island; *Aralia formosa* Heer occurs at Moletein and in the Bohemian Cretaceous as well as in the Dakota group and Raritan formation; *Aralia Zaddachi* Heer of the Baltic Oligocene occurs in the Californian Miocene; and *Aralia Looziana* Sap. & Mar. of the Gelinden flora reappears in the Fort Union group.

The genus is well represented both in the Cretaceous and Tertiary of Europe, Schimper in his *Paléontologie Végétale* (1874) listing 34 species, mostly, from European localities.

Heer describes two species from the Tertiary of Siberia, a simple leaflet and a lobed leaf of the *A. Saportana* type; while Ettingshausen notes the occurrence of Aralia in the Tertiary of Australasia. Many of these fossil species have merely a paleobotanical value. Thus Newberry identifies seven species at the single Raritan horizon of Woodbridge, N. J., four of which are described for the first time by him.[1] Still another Raritan species is Heer's *Aralia formosa*, which occurs in the upper layers at South Amboy, N. J. It is quite possible that Newberry's *A. polymorpha*, *groënlandica*, *patens*, *palmata*, and *rotundiloba* are all the varied leaves of a single species. In the Matawan formation,

[1] Flora of the Amboy clays. 1896.

which overlies the Raritan and with which it is closely related both geologically and botanically, there occur numerous Aralia-like leaves. I have identified[2] five species from this horizon, and the protean character of all of these mid-Cretaceous forms is emphasized when we find but two of these Matawan leaves referable to Raritan forms and these not entirely identical, while two others are entirely new.

Saporta would consider all the forms referred to Sassafras (Araliopsis) as included in the Araliaceae, but it seems to me that most of these leaves have stronger affinities in other directions. Ward would consider these Aralia-like leaves as referable to Platanus or its ancestral prototype. I have provisionally referred *Sassafras acutilobum* L. to Aralia.[3] Among the remainder of the American species of Sassafras, those which are not true species of Sassafras are related to Cissites or Platanus (Protoplatanus).

Three types of leaves have been referred to Aralia: (1) palmately three to seven-lobed leaves; (2) pinnately or ternately parted leaves; (3) simple leaves or leaflets.

Leaves of the first style, which concern us more particularly, may be briefly characterized as follows: Palmately 3–7 lobed, thick or coriaceous; petiole usually present and stout; margins entire or dentate; primaries 3–5 (7 in *A. dissecta*) generally rather stout, basal in ten species, sub-basal in ten species, and supra-basilar in fifteen species, doubtful in a few cases; lateral primaries when forked usually above their base, often present as basal sub-primaries; secondaries camptodrome in the entire-margined forms and craspedodrome in those which have dentate margins, both characters combined in some species; areolation obsolete, or square, or polygonal; base decurrent or cuneate in twenty species, rounded or truncate in fourteen species, doubtful in the balance, of which one is cordate and two or three are lobate. Young leaves may be entire-margined and three-lobed, while older leaves are dentate and five-lobed, which has caused a further duplication of species.

We may distinguish Sassafras, Sterculia, and Platanus,

[2] Flora Matawan formation. 1903. [3] BOT. GAZ. 34: 438. 1902.

which are oftenest confounded with Aralia, by the following characters:

In *Sassafras* the primaries branch from the midrib, usually a considerable distance above the base, which is decurrent and never lobate; the margins are entire; the texture is not coriaceous; sinuses margined, or secondaries at least showing some evidence of disarrangement in the region of the sinuses; secondaries camptodrome; the decurrent base usually margined.

Sterculia has usually petiolate coriaceous leaves with obsolete venation and conically pointed lobes; is palmately lobed, usually from below the middle; primaries usually three from the top of the petiole; base cuneate; margins always entire; secondaries becoming effaced near the margin, or bowed close to the margin.

In *Platanus* the leaves are large, thick, and palmately lobed, not deeply so, however, and the sinus always open; coarse leaves three-nerved from near the base; primaries and secondaries straight and stout; secondaries numerous, parallel, usually craspedodrome; margin never entire; lobes always broad; base sometimes lobate.

The American species of palmately lobed Aralias may be separated into five groups.

SECTION I.

Thick leaves fan-shaped in outline with long thick petioles; young leaves three-lobed; old leaves five-lobed; lobes narrow and pointed; base decurrent (except *A. Zaddachi*); sinuses narrow, extending more than half way to the base; margins dentate above with craspedrome secondaries, entire below with camptodrome secondaries; primaries three, stout, supra-basilar (except *A. Zaddachi*); lateral primaries forking some distance from the midrib; secondaries numerous and parallel. *Aralia digitata* Ward leads the way to the Green River species, *A. macrophylla* Newb., and by its lobate basal expansion shows its close relation to *Platanus basilobata* Ward.

This section includes: A. Saportana Lx., Dakota group; A. Saportana deformata Lx., Dakota group; Aralia sp., Dawson, Mill Creek; A. Welling-

toniana Lx., Dakota Tuscaloosa, and Raritan; A. digitata Ward, Fort Union group; A. Zaddachi ? Heer, Miocene.

SECTION 2.

Thick leaves rather orbicular in outline, with a long petiole (so far as it is known), lobes 3 to 5, broad and obtusely pointed, showing a tendency to become sub-lobate; base but slightly decurrent, generally rounded or truncate; sinuses open, extending about half way to the base; margins entire; secondaries camptodrome; primaries three, basal or sub-basal; lateral primaries unbranched, usually with sub-primaries below; areolation usually obsolete; smaller leaves than in section 1. A common type of mid-Cretaceous leaf is that which has been referred to *Aralia groenlandica* Heer and which has been recorded from the more or less synchronous strata of the Atane schists, the Dakota group, the New Jersey Raritan and Matawan formations, and the Island Raritan. I take as typical leaves of this species Heer's *f. 3. pl. 38* Fl. Foss. Arct. 6, abth. 2 and Lesquereux's *f. 1*, *pl. 54*, Fl. Dak. Gr.; and it may be noted that Heer includes leaves which are considerably removed from this type, while Lesquereux includes Dakota leaves (*fig. 2*, *loc. cit.*) which approach on the one hand his *Aralia subemarginata* and on the other (*fig. 3*, *loc. cit.*) leaves which approach the synthetic group of Aralias which Newberry describes from the Raritan formation of New Jersey. This *groenlandica* type of leaf seems to be a rather primitive one, a leaf from which numerous rather closely related species have been derived.

This section includes: Aralia groenlandica Heer, Atane, Dakota, Raritan, Matawan, Island; A. gracilis Lx., Laramie ?; A. notata Lx., Denver and Fort Union; A. patens, Newb., Raritan, Island; A. rotundiloba Newb., Raritan and Island; A. polymorpha Newb., Raritan; A. palmata Newb., Raritan and Matawan; A. subemarginata Lx., Dakota; A. Brittonianum Berry, Matawan; A. acerifolia Lx., Ft. Union and Miocene.

SECTION 3.

Mostly large, very coriaceous, fan-like leaves, with very stout petioles and primaries; lobes 3 to 5 or more (?); the lobes long and rather slender (except *A. Ravniana*), obtusely pointed; sinuses narrow, primary ones deep, extending nearly to the base; base

decurrent; margins entire; secondaries (when preserved) numerous, parallel, and camptodrome; primaries three, basal or sub-basal; the lateral primaries forking some distance above their base; areolation generally obsolete; the small basal sub-primaries of section 2 wanting. The extreme of form in this section approach very close to the *Saportana* type of leaf of section 1.

The species included in this section are: Aralia Ravniana Heer, Atane and Matawan; A. Towneri Lx., Dakota and Matawan; A. quinquepartita Lx., Dakota and Raritan; A concreta Lx., Dakota; A. angustiloba Lx., Miocene; A. Wellingtoniana Vaughanii Kn., Woodbine, Dakota; A Jorgenseni Heer, Greenland Tertiary.

SECTION 4.

This and section 5 are residuary groups of species that require further study. This section includes a rather heterogeneous assemblage of fan-shaped leaves which agree in having entire margins; pointed lobes; usually stout primaries; petiole (where preserved) stout; primaries basal or sub-basal; texture coriaceous or sub-coriaceous; secondaries camptodrome (where known). Medium sized or small leaves except *A. Whitneyi*, which is very large and seems to be the Miocene ancestor of the existing Tetrapanax of eastern Asia.

The species included are: Aralia Masoni Lx., Dakota; A. Mattewanensis Berry, Matawan; A. Westoni Daws., Mill Creek; A. rotundata Daws., Mill Creek; A. radiata Lx., Dakota; A. tenuinervis Lx., Dakota; A. Whitneyi Lx., Miocene.

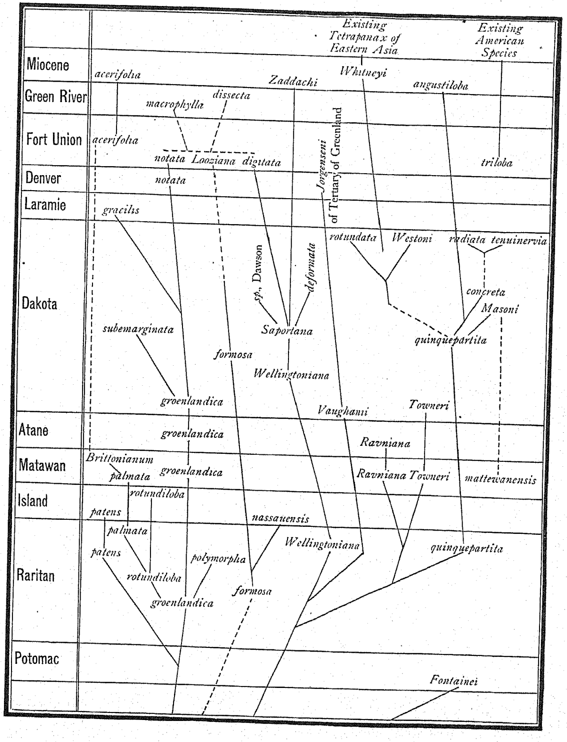
SECTION 5.

Rather small trilobate leaves with undulate or dentate margins; decurrent base; primaries three, stout, unbranched, sub-basal or supra-basilar; secondaries camptodrome and craspedodrome; lobes full, pointed. Includes leaves derived from the *Vaughanii-groenlandica* type and approaching the *notata-digitata* type of leaf very closely.

The species included are: Aralia formosa Heer, Dakota and Raritan (Europe); A. nassauensis Hollick, Island; A. Looziana Sap. & Marion, Fort Union (Europe); A. serrulata Kn., Fort Union.

SIMPLE LEAVES OR LEAFLETS.

The simple leaves referred to Aralia, following the precedent set by European paleobotanists, are four in number:


Existing Tetrapanax of Eastern Asia
Existing American Species
Miocene
Green River
Fort Union
Denver
Laramie
Dakota
Atane
Matawan
Island
Raritan
Potomac
acerifolia
Zaddachi
Whitneyi
angustiloba
macrophylla
dissecta
acerifolia
notata
Looziana
digitata
triloba
Jorgenseni of Tertiary of Greenland
notata
gracilis
rotundata
Westoni
radiata
tenuinervia
sp., Dawson
deformata
concreta
Masoni
subemarginata
Saportana
quinquepartita
formosa
Wellingtoniana
groenlandica
Vaughanii
Towneri
groenlandica
Ravniana
Brittonianum
palmata
groenlandica
Ravniana
Towneri
mattewanensis
rotundiloba
patens
nassauensis
palmata
Wellingtoniana
quinquepartita
patens
polymorpha
rotundiloba
formosa
groenlandica
Fontainei

Aralia Browniana Heer from the Tertiary of Greenland, which may be compared with European leaves from the Oligocene of St. Zacharie and the Miocene of Armissan.

Aralia transversinervia Sap. & Marion, described by Hollick (who notes its resemblance to Ficus) from Long Island as identical with Saporta and Marion's Gelinden leaf.

Aralia lasseniana Lx., from the Eocene (?) and Miocene (?) of California, which may be compared with leaves from the Sezanne flora.

Aralia coriacea Velen., identified by Hollick from Marthas Vineyard, the type from the Cenomanian of Bohemia.

SPECIES NOT INCLUDED in the foregoing sections are:

Aralia Fontainei Kn., from the Potomac, the remains of which are too poor for accurate diagnosis.

Aralia triloba Newb., which represents a ternately or pinnately parted leaf from the Fort Union group, which is evidently ancestral to the modern North American Aralias.

Aralia ? Waigattensis Heer, which represents a probably pinnate leaf of uncertain affinities from the Patoot beds of Greenland.

Aralia dissecta Lx., a large much lobed leaf from the Green River group.

Aralia Wrightii Kn., represented by incomplete remains from the Miocene of Yellowstone Park.

DOUBTFUL REMAINS include:

Aralia sp. Dawson, from the Mill Creek, which has been included with *Aralia Saportana* because Dawson thought that it might be that leaf.

Two forms of *Aralia* sp. determined by Knowlton from the Laramie of Wyoming; two by the same author from the Upper Eocene of the John Day Basin, Oregon; and one from the Miocene of Yellowstone Park.

The foregoing table shows the relationship of these leaves as I conceive them.

PASSAIC, N. J.

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

W. F. GANONG.

(*Concluded from p. 367.*)

B. MESOPHYTIC DIVISION (MESOPHYTIA) CULTURE SECTION.

Consists of plants requiring the normal climatic and soil conditions of this region, useful to man and kept by his care in certain definite artificial groups.

II. RECLAIMED SALT MARSH FORMATION (MEADOW FORMATION, POIUM).

Consists, in adaptation to the very fine and hence poorly-aerated but evenly-moistened soil, of slender-rooted surface-following and hence herbaceous plants, in this case grasses or grass-like plants useful for forage or grain. Owing to the peculiar conditions here prevailing in the form of a newly-opened field (see page 295), no care from man directly is necessary to keep the plants in their desirable economic condition, for both seeding and resistance to undesirable immigrants take place naturally as long as he preserves the field in its best condition.

Includes, within an enclosure of dikes, the greater part of the area of the original salt marshes, from the sea to the head of tide on the rivers, and extended artificially into the lakes of the bogs and the bogs themselves (page 179). The formation includes three associations.

4. THE PHLEUM-AGROPYRUM, OR TIMOTHY-COUCH ASSOCIATION, OR PHLEUMETUM.

The characteristic, prevailing and most valued association of the perfectly reclaimed marsh, occurring everywhere on the higher parts of the marsh within the dikes where the drainage is good, and where the marsh soil has not been exhausted or has

not roads nor bald spots (*figs. 7, 8*). Distinguished by its familiar hay-meadow aspect, though with an unusual prevalence of couch and unusual density, luxuriance and purity of the grasses.

The association is composed of two dominant members of nearly equal prominence, with several secondary and many subordinate members, and frequent visitors.

PHLEUM PRATENSE L. Timothy.—The most abundant, characteristic, and valuable plant of the reclaimed marsh, and the dominant member of the Phleumetum. It is confined to well-drained and salt-free places, but takes possession wherever these conditions are found, hence on the highest and oldest marsh, along ditch ridges and to some extent on dikes, particularly those not exposed to the dash of the sea, and reaching its greatest perfection on the banks of aboideaued creeks. In the reclamation of marsh it is the last of the natural sequence of forms and apparently can maintain itself indefinitely as long as the drainage is kept up. It is killed immediately by salt water.

A familiar vegetation-form, typical of the grasses. Its root-hairs are plasmolyzed by 30 per cent. or less of salt water. Not native; introduced from Europe.

AGROPYRUM REPENS Beauv. Couch.—Second to the preceding in abundance and luxuriance on the reclaimed marsh, and in places even exceeding and replacing it. It forms here a highly valued hay, little inferior to timothy. It extends also upon the dikes and is the characteristic dike-top grass, especially on the dikes exposed to occasional wash from the sea, including the old abandoned dikes on the salt marsh. It also tends to come in upon the highest parts of the Staticetum.

Vegetation-form very like timothy, but able to stand salter, though not wetter places than the latter. Its root-hairs endure 30 per cent. pure salt water without plasmolysis. A native plant, found also in Europe; doubtless the form on these marshes is introduced with the timothy from Europe.

AGROSTIS ALBA L. Brown top. (Includes also *A. vulgaris*, not now considered distinct.)—Distinctly third in importance of the forms of the reclaimed marsh, occurring intermixed with the two dominant forms, but tending to occupy especially the margins

of the drainage furrows, and the lower ground, where, especially on poor marsh, it often replaces entirely the other two and becomes the dominant form. Along the roads and in places somewhat salt, it is much dwarfed. It is one of the first forms to come upon the reclaimed marsh, following after the members of the Salicornetum and Staticetum.

Vegetation-form and adaptations not especially studied; evidently more halophilous and hydrophilous than the preceding.

TRIFOLIUM PRATENSE L. Red clover.—Occurs as a characteristic companion with timothy, under whose shade it thrives everywhere on the best marsh. It varies greatly in quantity in different years, sometimes being extremely abundant (locally "clover-years"), and sometimes being nearly wanting, perhaps because it is killed by some winters and requires two years to reach full maturity.

Vegetation-form and adaptations not specially studied, but its power of fixing nitrogen comes here into account, and possibly some relation of a remotely symbiotic sort exists between it and the timothy. It is immediately killed by salt water.

TRIFOLIUM HYBRIDUM L., alsike, and T. REPENS L., white clover, also occur, but less abundantly. The two former are introduced from Europe, but the latter is native.

CHRYSANTHEMUM LEUCANTHEMUM L. Bulls-eye daisy.—Abundant in places and somewhat gregarious, and in other places wanting. Apparently it cannot compete with the timothy and couch on the best places but comes in where conditions are less perfect for those two forms. Not native, but from Europe.

Other secondary forms of minor importaace are:

Alopecurus pratensis L., bastard timothy or Durgin timothy. Rather abundant in places, and an injury to the hay-fields through its early ripening.

Calamagrostis Canadensis Beauv., blue-joint, occurs in occasional patches, but belongs rather with the hydrophytic associations.

Poa pratensis L. Occasional.

Lolium temulentum L.

Danthonia spicata Beauv.

Agrostis scabra Willd. [*A. hyemalis* (Walt.) B. S. P.]

Lathyrus palustris L. Rather common in spots on good marsh.

Ranunculus acris L. Buttercup. In patches on poorer marsh, not abundant.

Other plants occurring amongst the grasses as subordinate members or visitors are: *Fragaria virginica* L., strawberry; *Achillea millefolium* L., yarrow; *Leontodon autumnale* L., fall dandelion; *Brunella vulgaris* L.; *Viola* spp.; *Cerastium* spp.; *Epilobium lineare* Muhl., *Rumex Britannica* L.; *Rhinanthus Cristagalli* L.; *Euphrasia officinalis* L.; *Aster Novi-Belgii* L.; *Lactuca leucophaea* Gray; *Solidago neglecta* T. & G. Along the ditches grows *Convolvulus sepium* L., and there are many others.

The general adaptations of these forms to this habitat are sufficiently plain; they are typical mesophytic grasses, and the reclaimed marshes offer, as has already been traced, a typical habitat for them. But when we pass to details, the subject is not so clear.

The two dominant members, the timothy and couch, occur variously intermingled, at times in about equal proportions and again with one or the other more abundant, even to such a degree that one may occur without the other for long stretches. No physical cause is traceable for these differences, beyond the fact that the timothy seems to have the advantage on the very best parts of the marsh, and the couch where salt is more abundant. Wherever they occur intermingled, patches of one or the other often exist without visible physical determinants; and their appearance gives the impression of a resultant of slight disturbances of equilibrium in the struggle between two evenly-matched forms (or else an adjustment between two mutually tolerant forms), here one and there the other, through the slightest causes, obtaining the advantage. Both plants seem to attain their greatest perfection and purity upon the banks of the aboideaued creeks, where no doubt the somewhat coarser soil, together with the better drainage, affords a better aeration for the roots, thus permitting the more luxuriant growth. At these and other places a marked phenomenon is to be observed, having no doubt an important bearing upon the nature of competition, namely, wherever these forms are most luxuriant, there the secondary and occasional forms are less abundant, and the latter come in with the decreasing vegetative vigor of the dominant forms. In the wetter, salter, and poorer marsh the Agrostis appears more abundantly, thus forming the marginal member in that direction, as couch does in the other; but in addition it forms in places on

low marsh great areas, to the exclusion of the dominant members, in such places becoming itself the dominant form. One cannot, however, trace all of the transitions to physical causes, and in places it seems as if we were dealing here with another case of unstable equilibrium, the forms acting in mass against one another. The same phenomenon appears in the bulls-eye daisy, groups of which appear amongst the dominant members in an apparently very irregular way, again suggesting that it is not physical causes alone which are responsible for their distribution, but that it is either the result of a struggle between nearly equally-matched masses of forms, or else that there is a large measure of pure accident in the details of their distribution relatively to one another. But of this we can know nothing until we learn how the forms "compete" with one another.

This association shows one very characteristic feature of an association, lacking in those heretofore considered, namely, a distribution of the aerial parts of its members in horizontal strata. Forming the uppermost layer in the full blaze of the sun come the two dominant grasses. Nestling below the shade of their leaves, come the clovers and the Lathyrus, while in a third layer nearer the ground are the leaves of the violets, strawberries, and other low forms which I have not tried to list, all of which, of course, blossom in the early spring before the grasses have grown tall. Here again we are faced by the question as to the real ecological interrelationships of these various forms, whether we have to do (1) purely with a mixture of forms, some of which happen to be able to live in the interstices left in the growth of other forms, or (2) whether the smaller derive some benefit from the shade or other protection of the taller, or (3) whether there may be some advantage to all the members from the association, such as we can imagine the taller timothy derives from the smaller but nitrogen-fixing clover. On these matters we still have no knowledge.

As above stated, the marginal member of the association towards the Staticetum is the couch, and the marginal member towards the Macrospartinetum is the brown top, while that towards the Cnicetum is the bulls-eye daisy.

Considering now the relation of this to the other associations, it is very important to note that it is the natural association for its situation, and has not to be brought into its typical condition nor kept there by the cultivation so necessary on the upland hay meadows. When a piece of marsh is diked and drained, there follows, as we shall later note, a perfectly natural succession of plants, from the Staticetum to the Phleumetum, without any care or seeding, and the Phleumetum therefore represents the best adapted type of vegetation in this region to the conditions of the reclaimed marsh. And it is important to notice that the timothy, and no doubt also the couch, are not native, but introduced forms. There were in this forested region no mesophytic native plants so well adapted to this new field as the open-ground hay grasses from Europe, a point in perfect harmony with the general principles controlling the relations of introduced to native plants as set forth by Gray in his essay "On the pertinacity and predominance of weeds." As long as the drains are kept up, and until by long years of cropping the soil begins to weaken, this association holds its own against all comers of every sort. There is no tendency here for forest to come in, as on the upland, for reasons already explained (p. 291), nor can the ordinary weeds gain a footing until the timothy weakens through exhaustion of the soil or other cause, in which case, some scanty approach to forest may occur (p. 293). On these marshes, therefore, these European hay-grasses find an even more congenial and competition-free field than upon the upland meadows. When, however, the drainage becomes imperfect, the brown top rises to prominence, and that in turn gives way to the broadleaf as the water becomes more abundant. In these phenomena of replacement we see illustrated the first principle of competition, that a form can hold its own only in the vicinity of its optimum, and beyond that it goes down readily before another form whose optimum is being approached.

5. THE ROADSIDE WEED ASSOCIATION, OR CNICETUM.

In addition to the "weeds" associated naturally with the Phleumetum, there occurs a distinct association of upland weeds in certain places on the marshes. As this association is by no

means characteristic of the marsh, being but an extension of that of the upland, where its consideration belongs, and moreover as it is of very subordinate importance in the marsh vegetation it need here be considered but very briefly.

On the marshes the association occurs only in places especially freed from salt. Thus it occurs especially along the inner slopes of the dikes, above the frequent zone of Atriplex, and below the capping of couch (*fig. 15*), that position being particularly well freed of its salt by the excellent drainage and protection from the occasional salt spray dashed against the outer face of the dikes. In such places occur Scotch and Canada thistles (*Cnicus*, giving name to the association), yarrow in great abundance, docks, strawberry, chickweeds and many others of characteristic appearance. Again, on the ridges of earth made by the mud thrown up from the ditches, the association again appears, but here, for reasons already explained (p. 293), it tends to include some shrubs, spiraeas, wild roses, rarely alders, and a few others, with occasionally small birches, almost the only situation indeed, in which any trees are able to exist upon the marsh. There is another situation in which the association is particularly well developed, namely, on the railway embankment built, but never used, across the marshes of the Shepody near the head of tide. On this embankment, built entirely of the marsh mud, the weeds have possession, and form a tangle of spiraeas, thalictrum, yarrow, bindweed, goldenrods, myrica, sorrels, lysimachia, evening primroses, and even some lichens, small white birch and others, a genuine upland association despite the marsh soil. Another situation in which the association is well developed is on the sites of the occasional hay ricks and the vicinity of the barns on the marshes. In the former situation the bindweed is especially characteristic, and in the latter the chickweeds, but in both cases many others are associated with them. At first sight these situations, directly upon the surface of the marsh, would appear too salt to maintain such a vegetation, but, as already explained (p 293), the conditions there are really such as to promote the removal of salt. Here and there among the Phleumetum some

of these weeds may appear, but never in any abundance. Finally there are those places on the flat shallow marsh already mentioned (p. 293), from which the salt appears to have been largely removed, where a growth of bushes with some weeds may appear. These spots are of some interest as showing the tendency of the marsh, when freed from the hindering influence of the salt, to develop the climatic type of vegetation for this region, namely, the forest.

C. HYDROPHYTIC DIVISION.

Consists of plants of various aspect, but typically of soft texture and small to moderate size, provided with abundant air system enabling them to thrive in part or in whole in standing water. Contains here four formations.

III. THE WET-MARSH FORMATION.

Consists of plants capable of enduring much but not constant standing water at the roots, but otherwise able to meet the conditions of the meadow; hence composed mostly of grasses and similar forms.

Occupies all places with constant capillary but only occasional hydrostatic fresh water, hence occuring in bands between the high marsh, whether reclaimed or salt, and the bogs, and coming in on reclaimed marsh wherever the drainage is neglected. It occupies very extensive areas, perhaps equaling the Phleumetum in extent and readily distinguished from the latter by the brighter green color of at least a part of it.

It is composed of two associations.

6. THE SPARTINA CYNOSUROIDES, OR BROADLEAF ASSOCIATION, OR MACROSPARTINETUM.

The characteristic association of the reclaimed marshes wherever drainage is poor but standing water is usually absent, and hence occupying great areas on the lower parts of the marshes away from the rivers and sea and between the Phleumetum and the bog (*figs. 7, 8*). The bad aeration of the soil permits the change to blue clay earlier discussed (p. 288), which seems usually to underlie the association. The association is readily distinguished to the eye by the large size, grace-

ful habit and bright green color of its dominant form, the broadleaf.

The association is composed of but a single truly dominant member but with several secondary forms.

SPARTINA CYNOSUROIDES Willd. Broadleaf.—Preeminently the character-plant of the reclaimed wet marsh, great areas of which consist of it almost exclusively. It occurs also around the margins of the freshwater lakes and streams, to a slight extent upon the matured Staticetum, along the tide-water and nearly fresh ditches, on the new mud of the lakes in reclamation and in the bottoms of aboideaued streams. It is of very great economic importance as hay, second only in value to the timothy and couch.

Its vegetation-form embraces the usual grass type, but with unusually large air-passages, luxuriant and markedly mesophytic structure, and a considerable power of salt resistance in its roots. Will stand considerable tiding. Its root-hairs endure nearly 50 per cent. of salt water without plasmolysis, and very likely have a specific power of resistance to the somewhat poisonous constituents of the blue-clay.

CICUTA MACULATA L. Called locally (by one person) caraway (sic).—Very abundant in places among the broadleaf, raising its upper leaves and flowers much above that form and so abundant that when in flower it gives the marsh a whitish look from a distance. It is a poisonous plant, but leaves and stems appear not to be injurious when dry, though horses have been supposed to have been poisoned by eating the roots.

CAREX MARITIMA O. F. Mueller. Watergrass or fresh-water grass.—The characteristic form where there is standing water in isolated places on the marsh, in such places often replacing the broadleaf, though usually more or less intermingled with it. It stands salt water well in tiding.

CALAMAGROSTIS CANADENSIS Beauv. Blue joint.—Occurs in places as a secondary member in the wet marsh, often in large closed patches, but especially along the ditches and toward the bogs, and along the courses of the streams in the bogs, where it sometimes grows in long, dense, closed masses. Also in places upon the dry marsh in the Phleumetum.

SCIRPUS ATROVIRENS Muhl. Kill-cow (sometimes three-square?). In the wettest places, and sometimes abundant, replacing the watergrass.

Of minor importance in this association is *Triglochin maritima* L., which occurs scattered amongst the broadleaf and watergrass, and appears as much at home as upon the Staticetum. Also there occur, in a subordinate rôle, *Thalictrum polygamum* Muhl., in occasional patches; *Epilobium lineare* Muhl., abundant in places; *Lysimachia stricta* L. [*L. terrestris* (L.) B. S. P.], abundant; *Iris versicolor* L.; *Campanula aparinoides* Pursh; *Scutellaria galericulata* L., and many others of lesser importance.

The power of the chief members to endure their wet situations is sufficiently explained by their capacity for air-storage, and their ability to stand some salt by their power of root resistance. Of these members at least three, *Carex maritima*, the broadleaf, and the Triglochin, are more or less halophilous, and it is at first surprising to find them thriving so well in this situation. It is very likely, however, that this position is more salt than it seems, for it must receive much of the drainage from the higher marsh (to which, as we have seen, much salt is being raised from below by evaporation), and this may be the case particularly in the low places where *Carex maritima* abounds. This can only be determined by analysis of the soil water in that situation. It may be possible, too, that a capacity to endure salt does not carry with it any lessened capacity to endure its absence, an important point still to be determined.

The broadleaf is the overwhelmingly dominant member of this association, no other approaching it in importance, and it often occurs for great areas practically pure. The Cicuta, raising most of its foliage above that of the broadleaf, is far the most prominent secondary member, but its exact relations with the broadleaf, whether of competition, mutual tolerance or mutual advantage, remain to be determined. The marginal member toward the Phleumetum is the broadleaf itself, as it is toward Staticetum. In the former case it meets the Agrostis, and in the latter appears upon the matured salt marsh, and no doubt in the original unreclaimed condition of the marshes it occupied the great areas between the Staticetum and the bogs. The marginal member toward the bog is sometimes the broadleaf and some-

times the watergrass. The association as a whole goes down very readily before the bog-marsh, which is constantly tending to invade it, and which has to be constantly fought by the marsh-farmers, partly by improving the drainage and partly by the admission of the tide.

7. THE CAREX-ASPIDIUM, OR BOG-MARSH ASSOCIATION, OR ASPIDETUM.

The characteristic association of the transition from Macrospartinetum or broadleaf, to bog,[43] occupying the places with constant hydrostatic water in the soil, but with little above it, resulting in a mixture of grass-like and bog-like plants. Where the transition from broadleaf to bog is gradual this band is wide, elsewhere narrow or wanting. It is marked by four dominant forms.

SPHAGNUM RECURVUM vars. PARVIFLORUM (Sendt.) Warn., and IMBRICATUM (Hornsch.),[44] with very likely others.—The most characteristic plant of this association, and the invariable leader of its advance upon the broadleaf.

CAREX FILIFORMIS L.—A very characteristic member of the association, often abundant enough to give it the appearance of a meadow. Vegetation-form not studied.

ASPIDIUM THELYPTERIS Swartz. *Dryopteris Thelypteris* (L.) A. Gray.—Very abundant and a characteristic member of the association. Vegetation-form and ecological characters not studied, but being in so aberrant a position for a fern, it offers an inviting opportunity for the study of a proper physiological life-history.

POTENTILLA PALUSTRIS Scop. *Comarum palustre* L.— Also abundant and characteristic, but not studied ecologically.

With these occur several secondary forms, inclining usually to gregarious patches: *Eleocharis palustris* R. Br.; *Equisetum limosum* L. (*E. fluviatile* L.); *Eriophorum vaginatum* L., and other sedges; *Epilobium palustre* L.; *Phragmites communis* Trin. [*P. Phragmites* (L.) Karst.], locally called "quills"; *Vaccinium oxycoccus* L. [*Oxycoccus Oxycoccus* (L.) MacM.], and others, together with visitors from neighboring associations.

Characteristic of this region also, and also occurring to some extent on

[43] Omitted from *figs.* 7, 8, because when those were drawn I had intended to include this association in part with Macrospartinetum and in part with Caricetum, but further study of the subject makes it seem best to treat it as a distinct association.

[44] Identified for me by Dr. C. Warnstorf, of Neuruppin, Germany, the leading authority in this group.

the Macrospartinetum, are certain shrubs, *Myrica Gale* and *Salix discolor*, of which the former persists upon the floating bog.

To this as to the following associations I have given but little study, and have little of value to offer upon them. It is an aggressive association, constantly tending to move up upon the broadleaf marsh, the transition to which is of the most gradual character. Of all the associations of the marshland, this has the least definite boundaries, and indeed there is some question as to whether it deserves distinct rank.

IV. BOG FORMATION.

Consists of plants capable of existence in stagnant but pure water, showing, unless immersed, marked xerophytic characters (including reduction in size both of entire plant and of its parts) in adaptation to the lessened power of water-absorption by roots exposed to low temperatures.

The bogs occupy the entire marsh country above the heads of the tide on the rivers, and also places between rivers where drainage is obstructed, but their area has been much reduced in the marsh country by artificial processes of conversion back to marsh (*fig. 2* and p. 179). It includes three associations.

8. THE CAREX-MENYANTHES, OR FLOATING-BOG ASSOCIATION, OR CARICETUM.

By far the most extensive and characteristic bog association of the marshland, occupying the old marsh surface from near the head of tide on the marsh rivers to near the neighboring uplands (*figs. 2, 7*). The transition from the Aspidetum to the typical Caricetum is perfectly gradual, so that it is difficult to place a limit between the two associations. The marsh, as earlier fully explained (p. 173 and *fig. 4*), falls away gradually from tide-head, so that leaving behind the high marsh with its Phleumetum we reach a somewhat wet marsh with its Macrospartinetum and a constantly wet marsh with its Aspidetum, and finally come to a marsh with constant standing water above the surface, and here begins the Caricetum. The characteristic dominant plants are sedges of several species whose copious interlacing air-storing rootstocks form a mat, which floats upon the surface of the water as it deepens (*fig. 4*), and which becomes three or four feet in

thickness. It floats upon a foot or two of water, beneath which is the true marsh mud, blue for a few inches from the surface, and below that red to the bottom. As a rule the bog is firm enough to walk upon, though it trembles beneath the tread, but in places it is unsafe.

The dominant plants are, of course, the sedges, chief of which are the following:

Carex filiformis L., and *Eriophorum vaginatum* L., from the preceding association, are equally or nearly as characteristic of this; also *Carex stricta decora* Bailey, *Carex Magellanica* Lam., *Eriophorum gracile* Koch, and others.

With these are associated as a principal though hardly as a dominant member *Menyanthes trifoliata* L., the Buck-bean, which is especially abundant on the margins of streams and ponds, and with it is *Calla palustris* L. Among the sedges occurs some Sphagnum, but this, in the floating bogs, is by no means a dominant plant.

Upon this floating mat grow many other plants, many of them distributed in groups the determinants of which are not plain. Thus, especially near the transition occur large areas of very abundant *Equisetum limosum* L.; in other places *Eleocharis palustris* R.Br., is densely abundant. Further out large areas are nearly covered with *Typha latifolia* L. (cattails); again groups of *Phragmites communis* Trin. (quills) occur. *Myrica gale* L. is also abundant. Among less abundant plants are *Juncus Canadensis* J. Gay, and *J. Balticus litoralis* Engelm., *Sparganium simplex* Huds., *Sarracenia purpurea* L., *Drosera rotundifolia* L., *Epilobium linearis* Walt., and a few others. But I have not attempted to make a proper ecological study of these bogs, which I hope upon another occasion to consider much more fully.

9. THE HEATH, OR FLAT (SOLID) BOG ASSOCIATION, OR ERICETUM.

I have not attempted to make any ecological study of this association. It occurs mostly around the margin of the Caricetum on the parts furthest from the sea, and between the rivers, as at Sunken Island (*fig. 7*), and is readily distinguished by the presence of abundant trees of larch and black spruce, and

the abundant heath bushes.[45] In places on the floating bog, especially near its margin, one sees occasionally dense mats of Hypnum several feet across, indicating no doubt the beginning of flat bog formation. In general this association occurs at the oldest part of the bogs and hence probably represents the conditions towards which the floating bog is tending. It tends to occur also in strips along the contact of mainland and the Macrospartinetum, where it begins to merge into swamp, as later to be noticed.

10. THE SPHAGNUM, OR RAISED BOG ASSOCIATION, OR SPHAGNETUM.

In a few places only, near the margin of the Caricetum, occur small areas approximating to the true raised type of bog, consisting almost entirely of Sphagnum rising above the general water level of the basin, with dwarfed heath bushes but no trees, and generally showing the characters of *Hochmoor* which I have already described in the first work of this series. Small areas of this character also occur in the Sunken Island. But I have not tried to work out their relations to other types of bog, and the subject remains for future study.

V. WATER MARGIN FORMATION (NEMATIUM).

The marsh and bog rivers above the influence of the tide everywhere exhibit a dense marginal vegetation (Typha, Sparganium, Acorus, Lysimachia, Chelone, Dulichium, etc.) differing in different parts of marsh or bog, and divisible into three or four associations. I have not, however, made any attempt to study these in detail. Another association exists on the margins of the lakes, and yet another in the bottoms of the aboideaued streams. There is also of course a plankton formation in these streams, but I have not studied it.

VI. THE SWAMP FORMATION (HELORGADIUM).

In most places, at the contact of reclaimed marsh and upland, occurs a region of poor drainage in the form of a narrow strip. On the wet marsh, along with the Macrospartinetum, this strip is

[45] Not all trees on the bog, however, indicate the flat bog, for many of them, as shown by soundings made by engineers of the Misseguash Marsh Co., are growing upon islands slightly submerged by the bog.

usually occupied by flat bog (Ericetum), but on the dry marsh it is more likely to form a strip of swamp, with alders, black spruce, and blue flag. This forms at least one association, probably more, but I have not attempted to study it, and it remains for future investigation.

The succession of the plants of the marshland in space and in time.

The succession of the plants of the marshland within associations, both in space and in time, and of the associations within the formations, have been described in the preceding pages, but we may here summarize the subject and attempt to represent it graphically. Then we must consider the natural succession which takes place in the reclamation of the marshes.

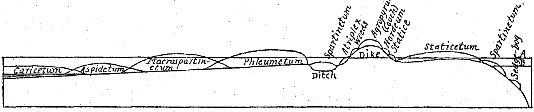


FIG. 15.—Diagram to show the distribution of the principal associations of the marsh land in relation to one another. The tops of the curves show the places of maximum development of the association, and the places where they overlap are the places of competition. *A* is extreme high tide level, and *B* ordinary high tide. The "ditch" is not a drainage ditch but one of those from which mud has been taken for the dikes.

The succession of the associations on the marshland is about as represented in *fig. 15*. The form given to each association is intended to represent its culmination at its optimum of size and vigor, and to show that the associations only mingle on their margins when their optima are past. These relations may be brought out in another manner and correlated with the distribution of the prepotent physical factors of water and salt, by means of the curves of *fig. 16*, which, however, it is to be remembered, are not constructed from actual measurements, but only ideally from observation. They have their chief interest as a prediction of the way in which such facts will ultimately be represented.

The distribution of the associations on the dikes is notable,

and needs some comments (*fig. 15*). The physical conditions upon the dikes are plain. The situation is a particularly well-drained one, but on the outer face of those exposed to the sea there must be more salt than upon the inner faces, due to the occasional wash of the sea at high tides during storms. At all events especially on the more exposed dikes, the outer slopes usually show a more halophytic facies than the inner. On both faces there is a distinct zonation, which differs somewhat in different places, but appears most characteristically, especially on dikes exposed directly to the sea or lower courses of the tidal rivers,

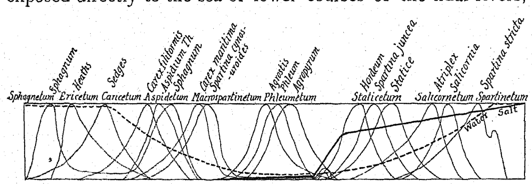


FIG. 16.—Diagram to show the distribution of the principal associations and of their prominent species in relation to the amounts of water and salt. The species curves show the approximate range of the forms within one another's habitat. The two members of the Macrospartinetum can endure some salt; hence their extension as here represented. The second summit of the Spartinetum represents the "sedge-bog."

to be as follows: On the outer face, the lowest zone, occupying the angle, is usually the Statice, but is sometimes Puccinellia; above this is a zone of Hordeum and above this the couch, the almost invariable dike grass, here evidently fully at home. Occasionally Atriplex occurs between Hordeum and couch. Now the Statice is the usual marginal member of the Staticetum, while the Hordeum comes in early upon that formation when maturing and the couch comes upon it later. There is plainly then upon the outer face of the dikes a general repetition of the order in the association, though the *Spartina juncea* is not, as far as I have noticed, in its place between Statice and Hordeum. The zonal arrangement, however, often shows Atriplex in place of the Statice, and the Hordeum may be wanting. On the inner face of the dikes, there is usually a band of Atriplex at the lower angle, especially when, as is usually the case, there is a row of

ditches containing stagnant and hence saltish water, just within the dikes, occupied by *Spartina stricta.* Above this Atriplex comes often, if not usually, a band of common roadside weeds, a part of the Cnicetum, while above it is the band and cap of almost invariable couch. This arrangement is sometimes different, and I have even seen a case where the top of the dike was occupied entirely by Atriplex, with a band of couch on each face of the dike below it, and other variants occur, the whole being much influenced by the position and age of the dike.

We pass now to consider another important phase of this subject, namely the natural succession of the plants on new marsh which is being reclaimed from the sea. It is rarely nowadays that a new piece of marsh is diked and reclaimed from the beginning, but what is practically the same thing occurs in numerous places, where the marsh is being renewed by the tide. When a piece or body of marsh shows a lessening of fertility, either through the growth of bog or other causes, the dikes are broken down and the tide admitted. The higher tides usually flow readily over it (an evidence, as I believe, of the gradual subsidence of the region), kill most or all of the vegetation upon it, and begin to deposit new mud. This is allowed to continue until several inches of mud have been laid down, a process requiring usually two or three years; then the dikes are re-built, the drains are opened, and the marsh is left to itself. A vegetation at once springs up upon it, which goes through a series of changes, ending in the development in four or five years of the Phleumetum or best timothy grass, and without any aid from man beyond keeping the drains in order. This succession can be followed in various places and is about as follows: When the tide first flows upon the marsh ,the plants show very diverse degrees of resistance to it. The bog plants, the various woody bushes, the clovers and the timothy are killed at once, it is said by a single tide. They turn white or brown and dry up, the bushes turning almost black, as if scorched by fire. On the other hand the watergrass, the broadleaf, the browntop, show a considerable degree of resistance, while the couch can stand

for some time on the higher tussocks.[46] I have not determined the exact cause of the death of these forms, but presumably it is due to the plasmolysis of the root hairs, and consequent loss of ability to absorb water, followed by a drying up. To this, of course, may be added some positively poisonous action of salt upon the protoplasm. The tide deposits layers of the rich mud, and upon this, while undiked, there tends to spring up a large development of the Salicornetum. In particular, there appears during the process of tiding an open growth of Suaeda, Salicornia, and Atriplex, all of which grow large and luxuriant. Of these the Suaeda appears to become most abundant, and is a large, diffuse, straggling plant quite superior to its small form on the river banks. The Salicornia also grows very luxuriantly, spreading diffusely in this situation. With these plants comes in some sedge, though I have not noticed that it becomes very abundant or luxuriant. Such appears to be the natural condition of marsh in reclamation. When the dikes are restored the first phenomenon observable is the large increase in size and abundance of these forms. They fill up the ground, and the Atriplex in particular grows even waist high. The remarkable luxuriance of the members of the Salicornetum under these conditions shows how far they are, upon the marshes, from occupying their optimum situation, from which they must be kept by the dominance of the other associations, a subject of much importance in connection with the nature of competition. But along with the increase in size, other forms immediately begin to come in, especially some members of the Staticetum, the *Spartina juncea*, Triglochin, and especially the Puccinellia, and the Hordeum, which is ubiquitous in such positions. Closely after these, however, comes the couch, and right after it the Agrostis. Such is the condition at the end of the first year, after which the timothy follows; and in the fourth year it becomes abundant. As the new forms come in the older tend to die out, so that finally, after a succession of forms answering to the natural succession in space on the marsh, the timothy takes natural

[46] This resistance is taken advantage of by some farmers, who admit the tide sparingly and are able to obtain some renewal without totally losing an annual crop. But it is not considered a profitable method.

possession, all the others except the couch disappearing. This, however, is the summit of the series; nowhere, excepting on the ridges along the ditches and in a few exhausted spots, where a low shrub vegetation appears, is anything higher developed. The timothy stands out as the best adapted plant in all this country to the conditions prevailing on the reclaimed marsh. In this process of reclamation, there is a grand opportunity to study the nature of competition, the problems of which, however, cannot be settled by observation alone, but must be attacked by experiment.

The above appears to be the normal succession upon places where high marsh is built; in the low places the succession is somewhat different, leading through watergrass ultimately to broadleaf, which by improvement in drainage may lead to couch and timothy. It is said by the farmers that the succession of plants depends much upon the way the drainage is managed.

There is another place in which the succession may be followed, namely in the lakes in process of reclamation, and I have seen it particularly well illustrated in Germantown Lake in Albert county, to which the tide is admitted by a canal. The tide has built into the lake long low points of marsh mud, which are at once taken possession of by a rank growth of *Spartina stricta* (sedge) immediately above which, on the higher parts, comes a dense growth of broadleaf. Right after the latter come scattered tufts of dense browntop, which is fairly abundant, and after this comes the couch. Here too is afforded a very favorable opportunity to study competition, which, however, I had not the time or means to utilize.

Conclusion.

The observant reader will not need to be told that the present study is highly defective and inconclusive, to a degree which no one can realize more than does its author. Yet this very defectiveness emphasizes an important lesson, for, while it is in part the fault of the author, it is not wholly so, but is in a large measure made necessary by the present imperfect state of our

ecological knowledge and methods. The study does make fairly clear, however, the directions in which research must now proceed, and upon this I desire to offer some comments.

The idea of ecological plant geography, the broadest and most important phase of ecology, is to interpret the physiognomy of vegetation; to tell precisely why each plant is where it is, in the company it is, and of the form, size, color, texture, etc. it is. Each plant, as it stands in nature, is an adjustment or equilibrium between its physiological powers and properties on the one hand, and the properties of the environment, physical and biological, on the other. Now, for a full understanding of these matters four principal things are needful.

First, a collection and description of the actual facts as to the kinds of plants which occur in a given region, as to their visible features, and as to the way in which they are grouped. Our present-day ecology, especially that which is being actively pursued in this country, is strong in this descriptive work, to which indeed it is well-nigh confined, and it is giving an excellent basis for future advance. In the present paper I think these facts about the marshland vegetation are fairly represented. Even from this point of view the study is defective in one respect, common to most of our ecological studies, namely, the descriptions apply to the summer only; if followed through the year (as it should, but for practical reasons could not, be), it might, and probably would, lead to conclusions somewhat different in details, as well as to much additional knowledge.

Second, an exact study and clear expression of the facts as to the physical features of the environment which can affect plant life. For the study of the physics of the atmosphere, the methods have been thoroughly organized by meteorologists, but we need some way of expressing meteorological results in a form for ecological use. It is very common in ecological papers, as in the present one, to give elaborate tables of temperature, precipitation, etc., and then to dismiss them with a few words of general comment. This shows either that meteorological data are obtainable more copiously and exactly than needful for ecological use, or else, as is more likely, they are not expressed in a

form in which we can make ecological use of them. Some advance has been made in this direction by such curves as Drude uses in his *Hercynische Florenbezirk* (p. 71), but these need further development. In the study of the physics of the soil, however, the ecological importance of which is becoming constantly more manifest, it is very obvious that, despite the rapid advances now being made, the methods of investigating and of representing the facts are still far from developed and wholly insufficient for ecological uses. The extension of knowledge in this direction is, I believe, the greatest desideratum of ecology for the near future. In thus emphasizing the deficiencies of our knowledge of the physics of the plant's environment from the ecological point of view, I would not underrate the positive knowledge we have, which is considerable. But it is notable that this knowledge is of a very general sort and not expressible in definite ecological form, as shown by the general and even hazy way in which it is commonly stated in current ecological literature, including the present paper. In fact, vague generalization and nimble guessing (much of it, no doubt, good guessing, but still guessing) are more characteristic of the physical part of our current ecological literature than is precise statement; and the expressions "probably," "doubtless," "in a general way," form a considerable part of present ecological language. All this is evidence that in our ecological discussions we have reached about the limit of possible advance with our present knowledge of the physics of the environment and of how to use the knowledge we have. Indeed, this point was reached some time ago, and much of recent ecological literature has been so barren of real advance as to bring upon ecology a reproach which it must be admitted it largely deserves. This is the more unfortunate since even the methods of ecological description have not substantially improved. I can say this with the greater frankness since my own study herewith presented so obviously reflects the prevailing formalism and deficiencies in this respect, though I have made some attempt to improve at least the method of description of the vegetation. There can be no question, I believe, that further substantial eco-

logical advance is not possible until we make a direct attack from the ecological standpoint upon the subject of the investigation and representation of the facts of the environment, especially of the soil. Now this obviously cannot be done, as most ecological work is now being done, by busy teachers who can devote to field work only a few weeks of their summer vacations. It can only be accomplished by the systematic work of trained investigators, who, with a fully and properly equipped laboratory established in the field at the place to be investigated, and with ample assistance to aid in the mechanical work, can devote their entire time to the subject for months or years until the problems are solved for that region. The laboratory must obviously be in the field, since the conditions vary so much in the different seasons and under the various local conditions. Thus, and thus only, I believe, can we make any further real advance in ecological plant-geography.

Third, there must be made a thorough study not only of the structure and development of the important plants which give character to the different parts of a vegetation, but also of their physiological characteristics quantitatively expressed. Thus, we need to know for each kind of dominant plant its transpiration power, and the extent of its possible regulation under various circumstances; its water-absorbing power; its capacity for air storage; its power and limits of resistance to salt or other unfavorable substances and influences; its cardinal temperature-points for growth and for its other physiological properties. For this study it is indispensable that methods and apparatus be developed by which the various facts may be ascertained with ease and precision, and the results expressed or represented in a form to make them available for ecological use, that is, so that they may be compared and correlated with the physical data. Very important in this connection is the determination of the physiological plasticity of the plant, and in how far adaptation to a new influence weakens or destroys adaptation to an older. Hitherto, in our studies of adaptation we have laid great stress upon the study of structures in relation to adaptation to environment, and much knowledge of this subject has been accumu-

lated, while physiological adaptation, the study of the accommodation of the protoplasm itself to outside influences, has received little attention. Yet this is the most important subject of all in adaptation; for structure, so far from representing the important feature in the adaptation of the plant to its environment, is simply an external manifestation of the way in which the protoplasm brings itself into better touch with the environment. It is an expression of a degree of physiological properties, and it is the properties and powers of the protoplasm itself which is the important thing. All such data are essential to the full understanding of the real nature of the vegetation-forms, those units of the ecologist; and in this direction, viz., the determination of physiological life histories of important plants, there lies not only an indispensable approach to future advance in ecology, but a most attractive field of research for its own sake. Such studies, and such only, will enable us to understand the true natural history of individual plants, and will help to bring the day when our "manuals," in addition to giving us the details upon which the classification of our plants is based, will give us also such information about their lives and habits as will enable us to understand their places in nature. These studies may in part be followed in university laboratories, but for the most part they can be carried on only in field laboratories, such as have already been mentioned as needful for the study of physical problems, and here both classes of problems, similar in general methods and inseparable in results, can best be investigated together.

Fourth, a knowledge of the true nature of plant competition and cooperation is essential. The fullest knowledge of the physical environment, and of the power of the plant to respond to it, would only enable us to explain the general situation and vegetation-form of plants in cases where each individual was free from any interference from others. But in fact, as we know, plants are rarely or never so situated, for, massing together, they profoundly affect one another's distribution and form. The study of vegetation, therefore, of masses of plants, involves this important element of their effects upon one

another. Or we may express the situation thus. Ecological plant geography is the study of the actual adaptations of masses of plants as they grow together in nature. The physics of the environment, plus the physiological properties of the plant, tend to give as a resultant a certain general vegetation-form; this, plus cooperation and competition, gives the actual groupings in a vegetation.

That plants do in some way compete with one another, that upon the same ground some kinds can drive others out and take possession, is, of course, evident to observation. That, on the other hand, certain kinds of plants can combine and cooperate for the common good is, I think, equally true. In both cases we know some of the general causes which determine the results of both competition and cooperation, but as to the details we know nothing. Seven years ago Warming, in his great book, said: "There is scarcely a more attractive biological field than to determine what the weapons are with which plants force one another from their positions," but today we know no more of that subject than when Warming wrote those words. Yet ecological plant geography cannot advance, nor can we understand the vegetation of a country or district, until we understand this subject, and we but blind ourselves and only imperfectly convince others by our present generalizations. The crucial point in competition is this: by what weapons or methods does one plant overcome another, when the result is determined between the plants and not by the environment. In a broad way we can often see general reasons why one plant should dominate another; the more rapid growth of one kind, or larger size, or the replacement of a shade-loving by a sun-loving kind, or the entrance of a new kind when one form has exhausted the needed minerals from a soil, etc., seem to give an ample explanation. But even in these cases, and especially in the many cases where the kinds seem evenly matched, we do not know precisely the method by which one kind manages to displace another. It is obviously by means of no visible carnal weapons such as animals use, nor is it a mechanical forcing aside of a weaker kind, for often there is ample standing room for the vanquished with the victor.

Some of the phenomena of competition seem to imply that each plant is able to control by some chemical or other method still unknown, a certain sphere of influence about it, a limited area of space of which it is the center and from which it can exclude others, and that this sphere of influence, like other adaptive features of the plant, is modifiable adaptively. Gregarious forms would be such as grow together so closely that these spheres touch, excluding other forms, and before the advance of such a phalanx other forms of lesser vigor must all go down. Elsewhere these spheres, rigidly maintained against an enemy, might be relaxed to admit a friendly or cooperating form, and other of the phenomena commented upon in the preceding pages, might find an illuminating explanation in such a conception. But it is all pure speculation, and can be settled only by careful field experiment. Until this is given we shall not know whether associations are mere mixtures, or are to some extent cooperative communities, and if the latter, what the nature is of the bonds which unite their members. I have no question that in a properly equipped field laboratory, such as has already been mentioned, competent investigators, working with an experimental piece of ground, could solve this most vital of questions. Fortunate will he be who first has the proper opportunity to attack it!

NORTHAMPTON, MASS.

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NOTES ON GARRYA WITH DESCRIPTIONS OF NEW SPECIES AND KEY.

ALICE EASTWOOD.

ANYONE who has done field work in California among the brush-covered hills will appreciate the puzzling character of Garrya. Like Salix, it is dioecious and is rarely found in flower and fruit at the same time, so that in the different herbaria of the country the species are quite inadequately represented and the types very unsatisfactory.

It is impossible with the present knowledge of the genus to attempt more than a provisional arrangement. The species bloom in the depth of the winter months, when few think of collecting plants; they fruit in August or September, when it is dangerous in many places to explore the dry hills on account of the scarcity of water and the density of the brush. In some years the fertile bushes bear no fruit and always seem few in comparison with the sterile ones, so that it is possible to pass through a region where these shrubs grow, at the right time of the year, without discovering a single plant in fruit.

For some time I have been interested in the two species that grow on Mount Tamalpais, across the Golden Gate from San Francisco. They seem to represent the two groups into which the Californian species fall. *Garrya elliptica* has peculiar pubescence, consisting of curly hairs which form a more or less dense tomentum on the lower surface of the leaves and young fruit. The berries, when ripe, are not unpalatable. The seeds are surrounded with an acid pulp which is very slightly tinged with bitterness. *Garrya rigida*, the other species, has fruit so bitter that one taste will suffice for a lifetime. This is commonly known as "quinine-bush." The pubescence is sparse and consists of almost straight, silky hairs, regularly appressed upward.

The genus may be divided into two great sections, the northern and the southern, the former characterized by non-branching aments; the latter with some or all of the aments branched,

generally near the base. There are also two kinds of pubescence in each class. In one the pubescence on the lower surface of the leaves is formed of curly or curly and wavy hairs intermixed to form a dense tomentum; in the other the pubescence, when present, consists of almost straight hairs, generally upwardly appressed and silky in texture.

In the following key these characteristics have been used to classify the different species, and, until they are better known in flower and fruit, it seems the only possible way and may perhaps accord with the natural affinities.

PROVISIONAL SYNOPSIS OF THE SPECIES OF GARRYA.

* *Aments not branched.*

Pubescence of tangled, curly, or wavy hairs.

Garrya Veatchii Kellogg Proc. Cal. Acad. **5**: 40.
Palmeri nom. nov.
undulata var. nov.
elliptica Lindl. Bot. Reg. *pl. 1686.*
Congdoni sp. nov.

Pubescence of upwardly appressed, almost straight, silky hairs.

Garrya buxifolia Gray. Proc. Am. Acad. **7**: 349.
flavescens Watson Am. Nat. **7**: 301.
pallida Eastwood Proc. Cal. Acad. III. **2**; 267.
rigida sp. nov.
Fremontii Torr. Pac. Rail. Rep. **4**: 136.
laxa var. nov.

* * *Some of the aments branched.*

Pubescence of curly hairs.

Garrya ovata Benth. Pl. Hartw. 14.
Lindheimeri Torr. Pac. Rail. Rep. **4**: 136.
macrophylla Benth. Pl. Hartw. 50.
oblonga Benth. Pl. Hartw. 50.
longifolia Rose (in herb).[1]

[1] This is doubtfully placed here. There seem to be two different species of Pringle's collection with this name, and I do not know which is the type. One seems too near *G. laurifolia*.

Pubescence of upwardly appressed, silky hairs.

Garrya laurifolia Benth. Pl. Hartw. 14.

salicifolia sp. nov.

Wrightii Torr. Pac. Rail. Rep. **4**: 136.

Fadyeni Hook. Ic. Pl. *pl. 333*.

GARRYA VEATCHII Kellogg.—Leaves ovate-lanceolate, acuminate at apex, rounded or oblique at base, entire or the youngest leaves very slightly undulate; upper surface except in youngest leaves smooth and shining, lower densely clothed with white tomentum consisting of short, very fine, closely curled hairs. Berries densely clustered and rounded at base without a sign of point or pedicel, apex beaked by the united base of the styles, calyx divisions minute, completely hidden amid dense hairs at top, a short distance below the styles.

The berries are so closely clustered and sessile that none of the involucres except the very lowest are visible in the type. The type was collected on Cedros Island by *Dr. Veatch* and is now in the Herbarium of the California Academy of Sciences.

GARRYA VEATCHII **Palmeri,** nom. nov. (*G. flavescens Palmeri* Watson Bot. Cal. **1**: 276).—Placed here on account of the character of the pubescence, which is that of *G. Veatchii* instead of *G. flavescens*. Distinguished from typical *G. Veatchii* by the broader leaves, generally oval, shortly acuminate or almost aristate, slightly undulate. Berries cuneate at base, the lower almost pedicellate; apex beaked by the united base of the styles and the two calyx divisions, which are prominent and close to the base of the styles; involucres even of the ultimate flowers easily distinguished and the lower conspicuously foliaceous.

The type was collected by *Dr. E. Palmer* at Milquatay, 60 miles (95^{km}) from San Diego on the road to Fort Yuma. This, as well as two specimens collected by *C. R. Orcutt*, one near Campo, Lower California (no. 900) and one from Hansons, Lower California, April 21, 1885, are in the Gray Herbarium. Here belong also no. 899 (*H. M. Hall*) collected on dry slopes in Lytle Creek Cañon, Southern California, April 24, 1898, and no. 2805 (*L. R. Abrams*) from the same locality, July 15, 1902.

GARRYA VEATCHII **undulata,** var. nov.—Differs from typical *G. Veatchii* in having oval or elliptical obtuse or aristate leaves

with undulate margins; berries cuneate at base and so densely clustered as to conceal upper involucres; calyx divisions hidden in dense wool and at some distance below the base of the styles.

This is represented in the Gray Herbarium by specimens collected by *O. D. Allen* at Pasadena, February 1885, and by a fragmentary specimen collected by *H. C. Ford* at Santa Barbara, April 1881. The best and most complete specimens have been collected by *George Grant* on Echo Mountain, back of the hotel. This mountain is a spur of Mount Lowe.

GARRYA ELLIPTICA Lindl.—This species is common in the Coast Mountains and extends from the Columbia River on the north to the southern part of the Santa Lucia Mountains on the south. Easily distinguished from other species by the large oval or elliptical leaves, strongly undulate. There is a great contrast between the almost smooth, dark green, glossy upper surface of the leaves and the white tomentose lower surface clothed with densely matted curly and wavy hairs. The calyx divisions are so small, so close to the pointed base of the styles, and so concealed by the dense wool that it is only by the most careful search that they can be found. The berry is abruptly short-acuminate at base. The bushes that grow in the inner range of hills have narrower and more pointed leaves than those that grow near the coast; but in all other respects seem identical.

Garrya Congdoni, sp. nov.—Stems brownish-red, youngest twigs white-tomentose. Leaves narrowly oblong to oval and elliptical, 3–5 ^{cm} long, 1–3 ^{cm} wide, tapering at both ends with recurved mucro at apex; petiole stout, keeled, 5^{mm} long; margins glabrous, thickened, entire or slightly undulate; upper surface glossy, yellowish-green, sparingly pubescent with curly or wavy hairs, the lower clothed with dense white tomentum consisting of curly and wavy hairs somewhat upwardly appressed but matted and tangled; veins distinct. Staminate aments numerous, varying in length; involucres cuneate at base, short-acuminate at each end with an obscure rounded tooth on each side of the middle, densely tomentose throughout, pedicels surpassed by the perianth; perianth with oval divisions united at top and clothed with long, wavy hairs.

Neither the pistillate flowers nor the fruits have been collected. The type was collected by *J. W. Congdon,* in whose honor it is named, near

Coulterville, Mariposa county, January 1898. Besides this, which was distributed by Mr. Congdon to various herbaria there is another specimen in the Gray Herbarium, collected by *Mr. Congdon* at Benton Mills, Mariposa county, July 5, 1898; also one in the Herbarium of the California Academy of Science collected by *Dr. C. Hart Merriam* on the Merced River, September 1902. A specimen collected by the author on the ridge between New Idria and Hernandez in San Benito county with immature fruit is also placed here. The young berries are rounded or abruptly pointed at base; the two calyx appendages are minute, closely appressed to the styles, and so densely clothed with long wavy hairs as to be hidden by the dense pubescence of the pointed base of the styles.

GARRYA BUXIFOLIA Gray.—Low, spreading shrub; leaves in typical specimens small, about 2^{cm} long, $1-1.5^{cm}$ wide, oval to elliptical or ovate, entire mucronate rounded or slightly oblique at base, the upper surface dark glossy green, lower densely white tomentose with almost straight silky upwardly appressed hairs; berries becoming subglabrous, beaked base of styles with small calyx divisions appressed.

The type was collected on Red Mountain, northern Mendocino county. Howell's specimens from Waldo, Oregon, have much larger leaves and smaller calyx divisions. It is abundant on the hills along the Crescent City road near Gasquet's.

GARRYA FLAVESCENS Watson.—Shrub with yellowish-gray aspect, young stems tomentose with a close, upwardly appressed pubescence of fine, almost straight, silky hairs; lower surface of leaves with similar pubescence, upper with scattered hairs irregularly appressed, Leaves broadly oval to narrowly elliptical, pointed at both ends, apex tipped with a sharp recurved mucro, veins strong and distinct; petioles $0.5-1^{cm}$ long; margin glabrous, entire.

The type specimen from the Gray Herbarium, collected by *Dr. E. Palmer* at St. George, southern Utah in 1887 (no. 183½), has unusually long and slender styles on the very immature fruit. A specimen from Kanab Plateau, collected by *Alfred Weatherill*, August 5, 1897, has fruit more mature, with the styles almost gone. On none of the berries examined could any trace of calyx divisions be found. This species seems to be confined to Utah and New Mexico and the adjacent country probably, but it is very near the next.

GARRYA PALLIDA Eastwood.—Distinguished readily in the field by the glaucous-gray tone of the entire plant, which does

not come from the pubescence but is noticeable where the leaves are almost smooth. Leaves large, oval to elliptical, entire, acute at each end with a recurved mucro at apex; petioles $1-1.5^{cm}$ long; pubescence sparse, upper surface of leaves generally glabrous except when young. Involucres deeper than in *G. flavescens*, being about 3^{mm} at the middle while the preceding is about 1^{mm}. Calyx divisions close to the beak of the base of the styles and concealed in the young fruit by dense hairs.

Grows in the Southern Sierra Nevada where *Pinus monophylla* is found or in the Coast Mountains where *Pseudotsuga macrocarpa* grows. Specimens are in the Herbarium of the California Academy from Kings River Cañon, San Emidio Cañon, Tehachapi, Kaweah Cañon, and Zaca Mountain, Santa Barbara county. The last-named specimens were collected by the author, June 1902, and have smaller, narrower leaves than specimens from other localities.

Garrya rigida, n. sp.—Erect shrub, $1-2^{m}$ high, with older stems gray-brown, becoming darker with age, youngest generally red though sometimes green, glabrous throughout except for a sparse, appressed pubescence on the younger stems, leaves, and bracts. Leaves elliptical-obovate, thick, coriaceous, entire, bright green, noticeably reticulate, 5^{cm} long, 2.5^{cm} wide on an average, tipped with an obtuse mucro, tapering at base to a thick petiole 1^{cm} long; petioles connate-clasping. Aments fascicled or sometimes solitary at the ends of the branchlets, $1-1.5^{cm}$ long or less, with 5–15 involucres connected by the peduncle which between each involucre becomes longer than the stamens; lowest involucres with recurved foliaceous tips as long as the body of the involucre, upper tipped with stiff points which diminish towards the ultimate flowers; body of the involucre green or red, generally tipped with green, pubescent at the middle and base. Flowers on filiform pedicels, $5-6^{mm}$; divisions of perianth green, 1-nerved, linear, white-hairy at top, 5^{mm} long, glabrous on inner side, united at tip, but later separating; stamens green, changing to yellow, with anthers 2^{mm} long, longer than the filaments. Pistillate aments rigid, $1-4^{cm}$ long, with the involucres closely imbricated and green, in other respects resembling those of the staminate flowers; flowers apetalous, 6 to each involucre, 2 styles to each pistil, black, narrowly subulate, sparingly clothed with

white hairs, as long as the ovary; ovary green, clothed sparingly at base and densely at apex with white upwardly appressed hairs. Fruit slightly pubescent, purplish-gray, densely clustered, very bitter.

Grows in the Coast Mountains of California and its range seems to be from Trinity to Monterey counties. The type locality is on Mount Tamalpais. It is quite abundant on what is known as the Bill Williams Trail from Eldredge Grade to Rock Spring, and has also been found along the railroad track.

This species has been included under *Garrya Fremontii* Torr., which is a species of the Sierra Nevada and the mountains of northern California and Oregon. The southern limit of *G. Fremontii* seems to be the Yosemite, where it is abundant along the road from Inspiration Point and also near Vernal and Nevada Falls.

Garrya rigida is different from *G. Fremontii* in habit, pubescence, inflorescence, and the fruits. Those of *G. rigida* are purplish, tinged with gray; those of *G. Fremontii* are black when dry.

It is much nearer *G. pallida* Eastwood, but differs in the bright instead of glaucous green foliage. Flowering specimens of *G. pallida* have not been collected, so good comparisons cannot be made; but the appearance of the two as they grow is quite different, as well as their range and environment.

Garrya Fremontii Torr.—Typically almost entirely glabrous, leaves rather small, not more than 4^{cm} long, and 2^{cm} wide, with cuneate base and mucronate apex. Staminate aments slender, with a few scattered hairs, more dense on the margins and near the tip of the two teeth. The stamens seem to be yellow and are exserted from the open sides of the sepals, which are united at the top. As the type has only staminate flowers it is impossible to compare the other parts with what seem the same species from other parts of the state.

The nearest of all the specimens in the Herbarium of the California Academy of Sciences is one collected by *C. A. Purpus* on Eel River, Mendocino county. This has much larger leaves but the staminate catkins are the same. Specimens from the Yosemite with immature fruit have the large leaves of the Eel River plants and almost sessile berries with inconspicuous calyx divisions. These characteristics hold true also with specimens collected on Mount Bohemia, Oregon, in the Callipoia Range, June 14, 1902, by *P. E. F. Peredes.*

Garrya Fremontii **laxa**, var. nov.—Distinguished from the forms included under *G. Fremontii* by the longer petioles of

the leaves, 2^{cm} or more, the more loosely fruiting aments, the peduncles more than twice as long as the involucres, and the pedicels equaling or surpassing the involucres. The berries, which turn black when dry, are tipped with the two styles and the conspicuously spreading calyx divisions opposite, giving the appearance of four styles when the stigmas have disappeared The pedicels in some of the staminate flowers are twice as long as the involucres, and in the fruiting aments vary from once to thrice as long.

This was abundant at Twin Lakes, the head waters of Cañon Creek, Trinity county, and was collected with immature fruit July 10, 1901. A single bush with dried staminate aments was found from which the comparison with the flowers of typical *G. Fremontii* was made.

Garrya salicifolia, sp. nov.—Stems slender, diffusely branched, marked and roughened by the lenticels; younger stems slightly pubescent. Leaves lanceolate, attenuate at each end, thin and coriaceous, veiny, glabrous or with few fine, scattered hairs chiefly on the margins, $3–6^{cm}$ long, $1–1.5^{cm}$ wide; petioles slender, $5–10^{mm}$ long, angled, pubescent. Aments erect in fruit, sparingly branched at base, slender, angled, slightly pubescent; bracts similar to the leaves but much smaller, $5–10^{mm}$ long, $1–2^{mm}$ wide. Berries globose, subsessile, generally two to each whorl, tipped when the styles fall away with a roundish, rough cap.

This is no. 259 Brandegee. It was collected at Sierra de la Laguna, Lower California, January 23, 1890. The smooth, willow-like leaves are very characteristic and sufficiently distinguish it from allied species. It is related and nearest to *G. laurifolia* Benth., but that has much larger leaves and differently shaped berries. It also approaches *G. longifolia* Rose, from which it differs in pubescence, foliage, and habit.

My most hearty thanks are due to Dr. B. L. Robinson, of the Gray Herbarium, Mrs. T. S. Brandegee, Mr. H. M. Hall, of the University of California, and Mr. Le Roy Abrams, of Stanford University, for the generous loan of valuable specimens.

BRIEFER ARTICLES.

THE TRANSPIRATION OF SPARTIUM JUNCEUM AND OTHER XEROPHYTIC SHRUBS.

(WITH TWO FIGURES)

It seems to be somewhat generally taken for granted that shrubs of decidedly xerophilous character, with early deciduous leaves and highly developed green cortex, must depend mainly on the latter for photosynthesis.

Grisebach makes the statement in regard to *Spartium junceum* L.: "At certain seasons this shrub develops little isolated leaves; these are of no physiological value whatever."[1] Kerner says of the leaves of the same shrub: "But these are of such secondary importance that their green tissue can form only the smallest portion of the organic substances necessary to the further growth of the plant, and this duty chiefly falls to the share of the cortex of the switch-like branches."[2] Other authors are less explicit in regard to the uselessness of the leaves of Spartium, but dwell much on the activity of the cortex.

Without more apparatus than was at my command it was not possible for me to investigate the relative amount of photosynthetic work done by the leaves and the cortex respectively. But it was a comparatively easy matter to ascertain the relative amount of transpiration accomplished by the leaves and by the cortex of the slender branches and twigs.

Young vigorous branches were taken and compared, two by two, until a pair of almost precisely equal area of cortex were obtained. This was not a difficult matter, as the form of all the branches is so nearly alike. One branch was then stripped of its leaves, and the scars left by their removal covered with melted beeswax, to which 5 or 10 per cent. of olive oil had been added, to lower the melting point. The freshly cut, larger ends of the branches were then submerged in water in test-tubes, which were fitted with corks, each with a double perforation, to admit the branch and a capillary tube for air to supply the

[1] Grisebach, Die Vegetation der Erde, Tchihatchef's French translation, 1:411. Paris. 1877. The German original is not to be had in Naples.

[2] Kerner, Pflanzenleben, Oliver's translation, 1:330. N. Y. 1895.

place of absorbed water. Tube and branch were then sealed into the cork with the beeswax mixture, and the leafy and the leafless branch thus arranged were placed out of doors for some hours in full sunshine, after being carefully weighed. Reweighing at the end of the period gave the loss of water.

On April 5 the leaves had not attained their full size, but nearly so, and were in excellent condition for the experiment. A branch 40^{cm} long had twenty-three leaves, with a total area (reckoning one surface only) of 17.5^{sqcm}. The area of the branch with its four twigs, was about 51.8^{sqcm}.

In three hours of sunshine, at a temperature in the shade of 20 to 22° C., the leafless branch lost 1.32^{gm} water and the leafy one 2.47^{gm}. The probable loss of water through the leaves of the leafy branch was therefore $2.47 - 1.32$ or 1.15^{gm}. Ratio of $\frac{\text{loss by leaves}}{\text{loss by stems}} = \frac{1.15}{1.32} = 0.87$. The ratio of the loss by unit area of the leaves to that by unit area of the stems would therefore have been about 0.87×3 or 2.61. It should be noted, however, that the upper epidermis of the leaves of Spartium contains a good many stomata and doubtless performs a considerable part of the work of transpiration, so that the value 2.61 is somewhat too large.

A repetition of the experiment on April 13, when the leaves had practically attained their full size (except in the case of a few at the tips of the branches), gave a loss of 3.24^{gm} for the leafy branch and 1.15^{gm} for the leafless one. The branches were for three hours in full sunlight at a temperature of 22° C. during most of the experiment.

The relative amount of transpiration performed by the leaves and the green cortex of this shrub is evidently not necessarily a measure of the relative amount of photosynthetic work. But it would seem probable that, since the leaves excrete a much larger amount of watery vapor in proportion to their area than the cortex does (and sometimes a larger total amount), they must also fix more of the carbon dioxid admitted to the tissues of this plant than the cortex does.

Some indirect evidence points very strongly in the same direction. Most of the growth of the Spartium in the neighborhood of Naples takes place between February 1 and July 1. I have no detailed numerical statement to make on this head, since the idea of taking measurements for the purpose did not occur to me until too late in the season. But two years' observation has made me sure of the fact above stated. Leafy individuals examined June 1 show branches 50^{cm} long

which have reached these dimensions since February. The leaves of the shrub first appear in considerable numbers about February 1, and they begin to turn yellow, preparatory to falling, about June 1. During the comparatively rainless period from late June until late September, the growth of the leafless shrub is extremely slight, and its obvious activity is almost wholly in the direction of growing and ripening the fruit.

In corroboration of the view that the photosynthetic work of this

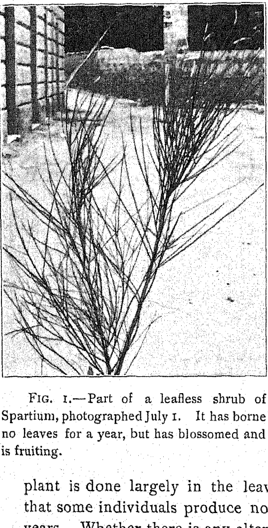

FIG. 1.—Part of a leafless shrub of Spartium, photographed July 1. It has borne no leaves for a year, but has blossomed and is fruiting.

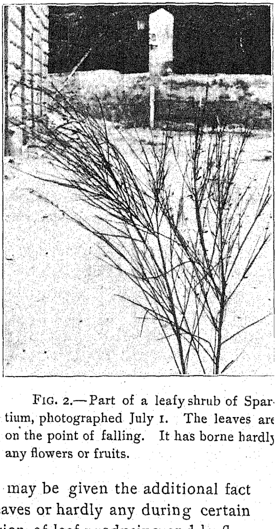

FIG. 2.—Part of a leafy shrub of Spartium, photographed July 1. The leaves are on the point of falling. It has borne hardly any flowers or fruits.

plant is done largely in the leaves, may be given the additional fact that some individuals produce no leaves or hardly any during certain years. Whether there is any alternation of leaf producing and leafless years for the same individual, I do not know. Now the leafless plants, at the end of May and beginning of June, when their neighbors are in full leaf and growing with great rapidity, are found to have made hardly any growth during the entire spring. But the leafless specimens often bear many flowers, and the leafy ones are comparatively flowerless. A glance at the accompanying figures will give some idea of the relative appearance of the two sorts of shrubs.

Time has not permitted the examination of the amount of transpiration accomplished by the leaves of the whole number of summer deciduous shrubs which occur in this region. Two of the most important species are *Calycotome villosa* Link and *Cytisus scoparius* Link. The former ot these gave on two successive days, with different specimens each day 2.6 times and 3.3 times as much loss from leafy as from leafless branches. The latter on different days and with different specimens gave 3.5 times and 3.1 times. These experiments were conducted exactly like those with Spartium.

My conclusions may be briefly summarized as follows:

1. In the three species examined, *during the leafy season*, the relative power of transpiration of the leaves as compared with that of the cortex is much greater, for equal areas.

2. During the leafy season, the total transpiration due to leaves may be more than three times as great as that due to cortex.

3. Photosynthetic work due to leaves is probably much greater during the leafy season and perhaps for the entire year than that due to cortex.

4. Leafless individuals of Spartium grow but little at any season.—JOSEPH Y. BERGEN, *Naples, Italy*.

GEASTER LEPTOSPERMUS: A CORRECTION.

IN the number of the BOTANICAL GAZETTE for October last, page 306, in the technical description of *Geaster loptospermus* Atk. & Coker, n. sp., occurs a typographical error in lines 14 and 22, the μ being used in place of mm. The measurements in these lines should read $3\text{–}4.5^{mm}$ and $2.5\text{–}3.5^{mm}$. In the general text the measurements were properly given, the error occurring only in the technical description.—GEO. F. ATKINSON, *Cornell University*.

CURRENT LITERATURE.

BOOK REVIEWS.

The Bonn text-book.

THE SECOND ENGLISH EDITION of the translation of what has come to be called familiarly the "Bonn" text-book—Strasburger, Noll, Schenck and Schimper's *Lehrbuch der Botanik*—has been revised to conform to the many changes in the fifth edition of the original work.[1] No other general text-book of botany has yet appeared that seems so nearly to meet the requirements of the university student. There is little evidence that the text was not originally written in English, and yet the style and characteristics of the original have not been lost in translating. The plan of the work, its main divisions into general and special morphology and physiology are the same as in the earlier editions, but the arrangement of the special topics has been made much more logical. Chapters have been recast and several entirely rewritten, either to incorporate recent investigations or to eliminate errors. In many instances original illustrations or reproductions from late monographs have replaced unsatisfactory figures. This is particularly true in the chapter which treats of cell division. The drawing of a typical vegetative cell (p. 51) which takes the place of the well-known figure with its bullet-like centrospheres, is much less likely to strain the student's credulity than its predecessor. There are helpful suggestions as to the selection of illustrative material, and of great value are the references in the text to the index of important literature on the special topics under discussion. The introduction, which is a succinct statement of the modern theory of evolution from the botanist's standpoint, has been revised to include DeVries's mutation theory.

From the point of view of the instructor, who often to his regret realizes the influence the printed page has upon the average student, one regrets that in a book of this sort more care should not be taken in the plants chosen for types. *Marchantia polymorpha* as usual is illustrated by several figures giving the important phases of its life history, whereas there are only habit sketches of Anthoceros and a Jungermannia form. It is difficult on this account to persuade a class that Spirogyra, Mucor, and Marchantia are not typical of the algae, fungi, and liverworts respectively.

At the risk of appearing captious, one is inclined to protest against the colored pictures which are so bad from every point of view that they are quite unworthy of a dignified book. Many modern morphologists will

[1] STRASBURGER, E., NOLL, F., SCHENCK, H., and SCHIMPER, A. F. W. A text-book of botany. Translated from the German by H. C. PORTER; 2d edition revised with the 5th German edition by W. H. LANG. 8vo. pp. ix+671. *figs. 686.* New York: Macmillan & Co. 1903. $5.

hardly agree with the statement (p. 158) that "flowers are the organs of sexual reproduction in plants," nor in the light of recent work done in physiological chemistry, can they affirm that "the physical attributes of air, water, and of the gases and metals used in the physical apparatus *can never* explain qualities like nutrition, respiration, growth, irritability, and reproduction." Only a teleologist or a poet would feel justified in saying that a membrane "has the power of decision whether a substance may or may not enter a cell." Occasionally one finds an error that has escaped the proof reader and is misleading. For example (p. 442) the embryo sac is described as "consisting of six cells which are formed in groups of three at each pole." Although these petty criticisms might be multiplied, they are inconsequent and need not be noted when the scope and high quality of the book as a whole is concerned.— FLORENCE M. LYON.

Ferment organisms.

THE TRANSLATION by Allan and Millar of Klöcker's book *Gärungsorganismen* (1900)[2] renders this work accessible to all English-speaking students, and places a valuable text-book in the hands of those interested in the microbiology of fermentation industries. In the discussion of ferment organisms and the history of their relation to industry, two names stand out with especial prominence, those of Pasteur and Hansen. Pasteur's discovery that bacteria were responsible for the diseases of fermented liquids led to the prevention of external infection, but could not be fruitful until Hansen had made practical application of his methods of distinguishing and securing pure yeast-cultures. In any text-book on fermentation organisms the results of investigations in the Carlsberg laboratory must therefore form an important part, and Klöcker, for years the assistant and distinguished associate of Hansen, is especially fitted to present these results.

The book is divided into three sections. The first of these, pp. 1–15, is introductory and historical; the second, pp. 16–169, describes the fittings and methods of a zymo-technical laboratory, with especial attention to the preparation of pure yeast-cultures, to Hansen's methods for preservation of yeasts, for preparation of spore-cultures, for analysis of top and bottom yeasts, and to his pure-culture system as applied to various fermentation industries. The third section, pp. 170–345, gives a brief but excellent systematic description of Eumycetes, including a general discussion of the structure, development, fermentation phenomena, adaptability, variation, and circulation in nature of Saccharomycetes. The text ends with a short description of those fission fungi which are related to alcoholic fermentation. Each section has its separate bibliography, and though this plan necessitates some repetition of titles, the critical and historical notes by the author on the more important works give the lists unusual interest and value.

[2] KLÖCKER A., Fermentation organisms, a laboratory hand-book. Translated from the German by G. E. ALLAN and J. H. MILLAR. 8vo. pp. xx + 392. *figs. 146.* London and New York: Longmans, Green & Co., 1903.

Although, like the briefer work of Jörgensen on the same subject, this book deals particularly with the malting and brewing industries, it will find an important place in many laboratories, both as a complement to the text-books which treat the chemical side of fermentation and as a systematic reference book.—MARY HEFFERAN.

Ferns.

THIS ELEGANT VOLUME [3] is intended primarily for amateurs and consequently is as free as possible from technicalities. An analytical key based upon the stalks is a principal feature of the book. In this key, the number of vascular bundles appearing in a transverse section of the stalk is the most important character. The chief divisions are those in which the cross section shows one, two, three, four, five, and more than five bundles, respectively. Other stem characters, such as the grooves, ridges, and color are prominent. There is also a key based upon the fructification. All the ferns of the northeastern states are figured and described, there being more than three hundred photographs, all of which are original. The photographs of sori, most of which are taken at a magnification of 5.5 diameters, are exceptionally fine and will be valuable not only to the amateur who is learning to identify ferns, but also to the teacher, who will find them useful in demonstration. In photographing the sori, a camera with a bellows extension of twenty-four inches was used, and the focal length of the lens was reduced by slipping over it a cheap copying and enlarging lens, thus giving the desired magnification.

While the book is addressed to amateurs and is written in popular style the author's acquaintance with ferns in the field, together with the peculiar key and excellent illustrations, will make it useful to the experienced botanist.—C. J. CHAMBERLAIN.

MINOR NOTICES.

PART 17 of Engler's *Das Pflanzenreich*, a volume of 326 pages, treats the Lythraceae by E. Koehne.[4]

GREEN[5] has revised his *Forestry in Minnesota*[6] and made it more applicable for general use. A very valuable part of the volume is a tabular classification of what is known of the sylvicultural habit and uses of the

[3] WATERS, CAMPBELL E., Ferns, a manual for the northeastern states, with analytical keys based on the stalks and on the fructification. 8vo. pp. ix+362. Illustrated, New York: Henry Holt & Co. 1903. $3.

[4] ENGLER, A., Das Pflanzenreich. Regni vegetabilis conspectus. Heft 17. Lythraceae: E. Koehne. 8vo. pp. 326. *figs. 59*. Leipzig: Wilhelm Engelmann. 1903. *M* 16.40.

[5] GREEN, H. C., Principles of American forestry. 12 mo. pp. xiii+334. *figs. 73*. New York: John Wiley & Sons. 1903. $1.50.

[6] BOT. GAZ. 34: 455. 1902.

important American timber trees. This will be much appreciated by students of forestry.—H. N. WHITFORD.

IN A VERY attractive volume Snow[7] discusses the species and properties of a large number of native and foreign species of wood. A valuable feature of the book is the half-tone reproduction of photographs of trees, bark, and wood of many species, usually one plate for each genus that is treated. The work is an untechnical presentation of the subject. It would have been wise to substitute modern terms for "exogenous" and "endogenous" in the text. —H. N. WHITFORD.

NOTES FOR STUDENTS.

SCHMIED reports[8] a carotin dissolved in oil in the periderm of the roots of *Dracaena reflexa*, which is identical in many respects (not in all), with the carotin of Dancus.

IN A WORKING PLAN for some forest lands in South Carolina Sherrard[9] gives data concerning the silvicultural habits of the southern pines in this state.—H. N. WHITFORD.

SCHWARZ[10] thinks the diminished flow of the Rock River is due to the deforestation of large tracts of land in its basin. Cultivated lands and wood lots have been largely converted to pasturage, thus interfering with waterflow. He advises a more careful treatment of the present forest and its enlargement where it will not interfere with land more valuable for agricultural purposes.—H. N. WHITFORD.

CHARPENTIER[11] finds that the green alga, *Cystococcus humicola*, grows luxuriantly in solutions, the air above which is lacking in CO_2. The necessary carbon in such cases may be taken from glucose. The green color may develop in the dark, though growth is less rapid in this condition. When required to depend upon atmospheric CO_2 as a source of carbon, the growth of Cystococcus is very slow.—H. C. COWLES.

A REPORT of the Bureau of Forestry of the Philippine Islands[12] contains

7 SNOW, H. C. The principal species of wood; their characteristic properties. 8vo. pp. xi+203. *pls. 39. figs. 4.* New York: John Wiley & Son. 1903. $3.50.

8 SCHMIED, H., Ueber Carotin in den Wurzeln von Dracaena und anderen Liliaceen Oesterr. bot. Zeits. 53:313–317. 1903.

9 SHERRARD, T. H., A working plan for forest lands in Hampton and Beaufort counties, South Carolina. Bull. no. 43, Bureau of Forestry, U. S. Dept. of Agric. pp. 54. *pls. 12. figs. 11. 1 map.* 1903.

10 SCHWARZ, G. F., The diminished flow of the Rock River in Wisconsin and Illinois, and its relation to the surrounding forests. Bull. no. 44, Bureau of Forestry, U. S. Dept. of Agric. pp. 27. *pls. 6. 2 maps.* 1903.

11 CHARPENTIER, P. G., Sur l'assimilation du carbone par une algue vertue. Compt. Rend. 134: 671–673. 1902.

12 REPORT of the Bureau of Forestry of the Philippine Islands from July 1, 1901, to September 1902. pp. 451–527. Report of the Philippine Commission.

some interesting matter concerning the condition of forestry there. There are between 600 and 700 native arboreal species of which there is some information, but there is great confusion in both scientific and popular names. Considerable work has already been done in ascertaining the condition of the forests in various parts of the Island.— H. N. WHITFORD.

ALEX. ARTARI, has been studying the relation of chlorophyll to light in some algae, especially Stichococcus.[13] The development of chlorophyll in the dark is possible only when the nutrition is good. Similarly chlorophyll often vanishes in the light under highly favorable nutrition conditions. Artari thinks that the disappearance of chlorophyll in the phylogenetic development of parasites is thus a matter of nutrition and bears no relation to light. —H. C. COWLES.

NĚMEC[14] has compressed the growing apices of shoots of *Nepeta macrantha*, and studied the effects on the leaf primordia. By preventing the growth of one the position of these is usually modified but in one experiment the phyllogenous tissue was extended beyond the normal. As was expected, the number of rows of leaves was not modified. It may be remembered that Vöchting found the number of rows of leaves of some cacti dependent on the illumination and changeable with it.—E. B. COPELAND.

V. KINDERMANN[15] has confirmed the results of Leitgeb and Molisch as to the resistance of guard cells, and added new data. Many agents were employed, such as acids, alkalis, harmful vapors, illuminating gas, desiccation, lack of oxygen, and in every case guard cells are found to be more resistant than other cells. They sometimes remain alive for several days after the death of other leaf cells. The author thinks this resistance is not referable to the cell wall, but is a property of the cytoplasm.—H. C. COWLES.

ED. GRIFFON, whose previous studies on chlorophyll are well known, has reinvestigated some of Boussingault's results,[16] from which it has been commonly supposed that the synthetic power of the palisade cells far exceeded that of the spongy parenchyma in ordinary leaves. The earlier results are confirmed in a general way, though the difference is much less than Boussingault thought. The maximum difference in favor of the palisade was found to show the ratio of 100 to 54 instead of Boussingault's 6 to 1. The ratio is

[13] ARTARI, ALEX., Ueber die Bildung des Chlorophylls durch grüne Algen. Ber. Deutsch. Bot. Ges. **20**: 201–207. 1902.

[14] NĚMEC, B., Ueber den Einfluss der mechanischen Factoren auf die Blattstellung. Bull. Internat. Acad. Sci. Boheme. 1903, pp. 14.

[15] KINDERMANN, V., Über die auffallende Widerstandskraft der Schliesszellen gegen schädliche Einflüsse. Sitzb. Akad. Wiss. Wien. Math.-Nat. Classe, Abth. I, **111**: 490–509. 1902.

[16] GRIFFON, ED., Recherches sur l'assimilation chlorophyllienne des feuilles dont on éclaire soit la face supérieure, soit la face inférieure. Compt. Rend. **135**: 303–305. 1902.

100 to 92 in the almost homogeneous mesophyll of the bamboo leaf.—H. C. COWLES.

THE EMBRYO-SAC of two sterile hybrids is discussed in a recent paper by Tischler.[17] The hybrids are *Ribes Gordonianum* Lem. (*R. aureum* × *sanguineum*) and *Syringa chinensis* (*S. vulgaris* × *persica*). Both parents of *R. Gordonianum* have normal embryo sacs with conspicuous nutritive tissue in the chalazal region of the ovule. In the hybrid this nutritive tissue is lacking and the development of the embryo sac is usually checked long before it reaches the fertilization period, the megaspores often failing to germinate at all.

In the parents of *Syringa chinensis* the nutritive tissue is in the form of a jacket derived from the integument and surrounding the embryo sac, which in both cases is normally developed. In the hybrid the nutritive jacket is more highly developed than in the parents, but the embryo sac becomes disorganized quite early, so that the stage at which fertilization might occur is seldom or never reached.

References are given to the few cases previously described of irregularities and imperfections in the development of the ovules and embryo sacs of sterile hybrids.—C. J. CHAMBERLAIN.

P. D. BUCK[18] has made a comprehensive study of the stomata and aeration tissues of a large number of Swiss plants, especially those of beech woods. A number of modifications of Schwendener's types are described, together with a new type, that of *Ranunculus acer*. Buck describes a number of variations on the same individual, especially differences in the level of the guard cells. While some groups, such as conifers, sedges, and grasses, are characterized by a definite structural type, it is more common to find rather a relation to the form of the leaf, or to the habitat. Perhaps his most interesting contribution deals with subterranean stomata, of which he finds three types: functional, functionless, and latent. The latent stomata attain full development only when the shoot which bears them comes above the surface. For the functional subterranean stomata, Mohl's theory as to the mechanism, of course, cannot be held, as there is no chlorophyll or synthetic activity, though starch is present. They were found to open and close like ordinary stomata when the moisture content of the air was changed. The last section of the paper deals with the spongy parenchyma, of which several types are noted.—H. C. COWLES.

THE U. S. Bureau of Soils in a recent bulletin[19] presents a comprehensive study of the influence of soil chemistry upon crop production. It is shown

[17] TISCHLER, G., Ueber Embryosack-obliteration bei Bastardpflanzen. Beih. Bot. Centralbl. 15: 408–420. *pl. 5.* 1903.

[18] BUCK, P. D. Beiträge zur vergleichenden Anatomie des Durchlüftungssystems. Inaugural Dissertation. Freiburg i. d. Schw. 1902. pp. 93.

[19] WHITNEY MILTON, and CAMERON, F. K., The chemistry of the soil as related to crop production. Bull. 22, Bureau of Soils. U. S. Dept. of Agric., pp. 71. 1903.

that in practically all cultivable lands no such influence exists. The soil water is at all times nearly saturated with the difficultly soluble minerals of which the soil is composed, and several hundred analyses of water from soils of every type and degree of fertility showed in almost every case that the materials essential for the plant are present in considerable excess of the amount required for the production of good crops. This result agrees well with the observations of students of physiographic ecology, that the chemical composition of the underlying rocks is of little significance in determining the development of vegetation, and it furnishes a sound basis for the explanation of this observed fact. It also emphasizes the importance of the study of soil physics, since it is in the physical properties of the soil that we must find the explanation of the important influences of soil upon vegetation. There are brief chapters upon the influence of climate, of texture of the soil, and rotation upon the yield of crops, and upon the rôle of commercial fertilizers. In an appendix is a concise description of the methods used for the quantitative determination of the various ingredients of soil waters. This will be greatly appreciated because of the simplicity of the apparatus, the ease of manipulation and the accuracy of the results.—G. H. SHULL.

IN THE RUST, *Coleosporium sonchi-arvensis* Lév.[20] during certain stages in the life history the cells contain two nuclei and at other stages but one nucleus. The uredospore and the cells of the mycelium to which it gives rise, contain two nuclei which divide by conjugate division, *i. e.*, each nucleus contributes to each of the two daughter-cells. The teleutospore produced from this mycelium is the last binucleate cell of the series. The two nuclei of the teleutospore fuse, after which the teleutospore at once germinates into a four-celled promycelium, each cell of which contains but a single nucleus. Each of the four cells of the promycelium produces a uninucleate sporidium. The first division of the nucleus of the sporidium is not followed by cell division, but starting with the sporidium there is developed a mycelium of binucleate cells. In short, from teleutospore to sporidium the cells are uninucleate, and from sporidum to teleutospore, binucleate.

The two nuclei which fuse in the teleutospore have maintained a separate existence throughout almost the entire life cycle of the host, and there is some evidence that the chromosomes, in the division of the fusion nucleus, are collected into two groups representing, possibly, the chromosomes of the male and female nuclei. While there is no proper cell fusion, the union of nuclei more or less separated in origin is not out of harmony with our conception of sexual reproduction in other groups of plants.—C. J. CHAMBERLAIN.

RUHLAND has presented in full[21] the results of his studies on several of

[20] HOLDEN, R. J. and HARPER, R. A., Nuclear divisions and nuclear fusion in *Coleosporium sonchi-arvensis* Lév. Trans. Wis. Acad. Sci. 14: 63–82. *pls. 1–2.* 1903.

[21] RUHLAND, W. VON, Studien über die Befruchtung der *Albugo Lepigoni* und einige Peronosporeen. Jarhb. Wiss. Bot. 39: 135–166. *pls. 2.* 1903.

the Peronosporales.[22] *Albugo Lepigoni* is near the level of *A. candida* in the interesting series of species in this genus, or if anything, more highly specialized, chiefly on account of its extraordinarily large and well differentiated coenocentrum. Ruhland agrees with Berlese and Wager that *Peronospora Alsinearum* has a uninucleate egg and well differentiated coenocentrum; and with Stevens that there is in *Sclerospora graminicola* a rather vague area of denser protoplasm in the center of the egg in place of a clearly defined coenocentrum, though otherwise it is very much like Peronospora. *Plasmopara densa* entirely lacks a coenocentrum and therein differs from *Plasmopara alpina* as recently described by Rosenberg. Ruhland observed a specimen of Plasmopara in which two mature oospores and a younger egg lay side by side, making three differentiated regions of ooplasm in the same oogonium. Such conditions might prove very interesting if one could follow the developmental history.

Ruhland discusses a number of the topics which the reviewer has recently treated in his paper on Saprolegnia. He agrees that the uninucleate egg in the Peronosporales is at a higher level of sexual differentiation than the multinucleate; criticises Trow's comparison of the coenocentrum to a "whirlpool in a river;" holds that the nuclear divisions in the oogonium are not established as reduction divisions; and is not willing to accept Rosenberg's recent comparison of these mitoses to the divisions in the spore mother-cell. —B. M. DAVIS.

A DISCUSSION has arisen over the characters of the genus Monascus. Ikeno[23] calls in question the identity of the form whose ascocarp has been recently described by Barker.[24] Monascus has formerly always been included among the Hemiasci. Barker found in his type a curious but nevertheless well-established system of ascogenous hyphae developing from the fertilized ascogonium, which clearly removes this form from the Hemiasci and so confident was Barker of its identity with other material of the same name that he regarded the entire genus as true Ascomycetes. Ikeno is not able to find ascogenous hyphae in the form which he considers *Monascus purpureus*. The ascogonium develops directly into a large cell, which becomes loosely invested by surrounding hyphae, and the spores arise by free cell formation within this—processes typical of the Hemiasci. Ikeno then holds to the old characters of Monascus and regards Barker's form as entirely distinct from this genus and a typical ascomycete. It is unfortunate that Ikeno does not present a full account of the period when the fertilization of the ascogonium should be expected and the stages of development immediately following this event. This is exactly the time when ascogenous

[22] See notice of preliminary paper, BOT. GAZ. 35:221. 1903.

[23] IKENO, S., Ueber die Sporenbildung und systematische Stellung von *Monascus purpureus* Went. Ber. Deutsch. Bot. Gesells. 21:259–269. 1903.

[24] Ann. Botany 17:167. 1903.

hyphae, if present, would be most easily found. As Barker states, there is little trace of their presence in later stages when the spores are formed. The account of Ikeno is, however, very positive as to the entire absence of ascogenous hyphae, and it is hard to see any place for them in the series of figures that he presents. Barker and Ikeno must either have had very different organisms, or there is a slip somewhere in one of the accounts of these authors.— B. M. DAVIS.

OLIVER[25] characterizes the Paleozoic gymnospermous seeds by the importance and dimensions of the pollen chamber and the complicated vascular system which embraces the body of the nucellus. He considers chiefly the cordaitean genus Stephanospermum, representing Brongiart's Radiosperms, and Cardiocarpus representing the same author's Platysperms, both from the French Permo-carboniferous. The latter possess many cycadean features, such as the relatively small pollen chamber and the thickening of the cells of the beak of the nucellus. They are more archaic, however, than the former. While paleobotanical terminology denominates these remains "seeds," they are usually preserved at a stage just preceding fertilization, and therefore answer to the modern unfertilized ovules. He next considers the genus Lagenostoma from the Lower Coal-measures of Lancashire and Yorkshire, chiefly as exemplified by *Lagenostoma ovoides* of Williamson. It is small and circular, and has a chambered apex with vascular prolongations which are quite unique. It resembles Cycads in the considerable area of "fusion" between the nucellus and testa, as well as in the presence of vascular strands in the plane of fusion. The confined form of the pollen chamber marks an advance in precision on the open type of the ordinary Paleozoic seeds. Modern cycadean structures are considered, as shown in *Cycas Rumphii*, and the paper closes with an examination of the modern species of Torreya, which, though siphonogamous as in all other conifers, still retains marked traces of the fertilizing contrivances that became obsolete when siphonogamy appeared.

Oliver also records[26] the discovery that the *Sporocarpon ornatum* of Williamson is really a transverse section of *Lagenostoma physoides* of the same author.

He also notes[27] a fungus on the fronds of Alethopteris from the Stephanian of Grand Croix, and of chytridineous sporangia in the nucellus layers of Sphaerospermum from the same formation.— E. W. BERRY.

VARIATION in the number of stamens of *Alsine media* L. has been studied during several years by Reinöhl,[28] using a combination of the statistical and

[25] OLIVER, F. W., The ovules of the older gymnosperms. Annals of Botany 17:451–476. *pl. 24, fig. 20.* 1903.

[26] OLIVER, F. W., New Phytologist 2:18. 1903.

[27] OLIVER, F. W., New Phytologist 2:49. 1903.

[28] REINÖHL, FRIEDRICH, Die Variation im Andröcium der *Stellaria media* Cyr. Bot. Zeit. 61[1]: 159–200. *pls. 2–4.* 1903.

experimental methods. Field studies showed that the stamens vary from 0 to 13, forming a bimodal curve with principal maximum on 3 and secondary maximum on 5. The relative prominence of the maxima, the value of the mean, and the coefficient of variability depend upon habitat and time at which collections are made. Although in nature the curve was always bimodal, three of the cultures produced asymmetrical monomodal curves which agreed with Pearson's theoretical type IV, in one instance the asymmetry being so slight as to give essentially the Gaussian probable error curve. This reduction to a homogeneous condition is an unusual result where the homotyposis of organs which have their origin in relation to the phyllotactic spiral is involved. The maximum on 5 was found to be completely eliminated in the third generation of plants grown in diffused light, while that on 3 was eliminated by the high manuring of plants which had been observed to have already a strong development of the higher mode. By still higher manuring he secured a curve with a strong maximum on 5 and a slight one on 8, showing thus by the maxima on 3, 5, 8, a perfect agreement with the Schimper-Braun series. Of the external factors light intensity was found to be the most important, and the richness of the soil in available foods next.

Finally it was found that in all cases the modal condition changes as the flowering season advances, the number of stamens beginning low, reaching its maximum only after some time, and falling again near the end of the season. This contravenes Burkill's[29] conclusions, which rest upon occasional collections aggregating less than 400 flowers cultivated in pots in a tropical greenhouse, while Reinöhl has observed 44,542 flowers, including in the case of cultures all the flowers produced during the flowering season. It also differs from observations by the reviewer[30] on *Aster prenanthoides* Muhl., the reason probably being that in *Alsine media* the height of vegetative activity is not reached until some time after the flowers begin to bloom, while in *Aster prenanthoides* the maximum vegetative activity precedes the development of the flowers.—G. H. SHULL.

E. HEINRICHER'S studies of the green half-parasites[31] have advanced considerably the boundaries of our knowledge. It was to have been expected that a group like the Rhinanthaceae, apparently half way on the road to holoparasitism, would yield results of surpassing interest. In his earlier paper Heinricher presents studies on *Odontites Odontites*, *Euphrasia stricta*, and *Orthantha lutea*. He finds that germination is independent of host stimuli, but that haustoria require a host stimulus in order to induce development. Odontites was brought to a state of flower and fruit entirely without parasitic nutrition, while Euphrasia could nourish itself to a much less degree.

[29] BURKILL, On some variations in the number of stamens and carpels. Jour. Linn. Soc. Bot. **31**: 220 *et seq.* 1895.

[30] SHULL, G. H., Amer. Naturalist **36**: 111–152. 1902.

[31] HEINRICHER, EMIL, Die Grünen Halbschmarotzer. Jahrb. Wiss. Bot. **31**: 77–124. 1898; **32**: 389–452. 1898; **36**: 665–752. 1901; **37**: 264–337. 1902.

Any species grows better in dense cultures than alone, showing that stronger individuals grow parasitically upon the weaker. Still stronger individuals result when the normal host plants are supplied. The species which have the greatest autophytic power have abundant root hairs, while the more fully parasitic forms are without them.

In his second paper Heinricher showed that the Rhinanthaceae require light for their development even more than they require a host. Synthesis of carbohydrates was shown by Sachs's iodin test. Various species of Euphrasia differ widely as to their parasitism, some being as independent as Odontites, while some absolutely require a host for full development. His third paper dealt with Bartschia and Tozzia, the forms which come nearest to holoparasitism. In Bartschia haustoria appear in the seedling stage, there are no root hairs, and a bud for the second growth period does not appear unless a host is supplied. Tozzia is the most remarkable form of all. It requires the stimulus furnished by a host root even for germination, differing in this from all other Rhinanthaceae and agreeing with holoparasites like Orobanche and Lathraea. For more than a year the plant lives wholly underground as a holoparasite, while late in the second season a tiny green shoot appears which soon flowers and fruits. Even this plant was shown to have some photosynthetic activity, though less than in any other member of the family. Bonnier found no active photosynthesis in these plants, and more recent authors have been inclined to doubt Heinricher's results. Apparently Heinricher has clinched his case by employing cut shoots and finding synthesis to take place there, although he uses the iodin test rather than the more accurate method of gas determination.

In his last paper Heinricher shows that chlorosis depends upon the lack of iron in the seed, not upon the more complete parasitism of the individual in question, as he at first supposed. In other respects, also, he finds differences in the properties of seeds in the same species, showing that all of one species do not have the same hereditary characters. Wide individual variations are also found to be due to differences of habitat. Strong host plants, for example, permit a better development of parasites. Heinricher is inclined to explain a number of Wettstein's species, especially his aestival and autumnal species, as true habitat variations. As might be expected, this view has called forth a series of polemics[32] which need not be mentioned further.

Heinricher's work gives us a basis for theorizing as to the origin of parasitism, since we find every step in the series within one group of plants. Apparently root hairs are soon lost, the first demand on the host being for raw materials rather than for organized foods. Further parasitism is acquired by drawing upon these organized foods, a process which is ultimately followed by the loss of chlorophyll and photosynthetic power.—H. C. COWLES.

[32] Jahrb. Wiss. Bot. **37**: 685–697. 1902; **38**: 667–688. 1903. Also Oesterr. Bot. Zeits. **52**: 246–249. 1902; **53**: 205–223. 1903.

NEWS.

DR. E. ULE has returned to Berlin with rich collections from South America.

DR. EUGENE ASKENASY, honorary professor of plant physiology in the University of Heidelberg, died recently.

THE *Revue Générale des Sciences* for October 30 contains a full account of the life and work of the late Professor Cornu.

DR. ANTON HANSGIRG, of Prag, has retired after forty years' service as professor of botany in the Imperial University of Bohemia.

DR. E. B. COPELAND has been appointed "systematic botanist" by the Philippine Commission, and sailed November 10 for Manila.

AMERICAN GARDENING announces that Mrs. Phoebe Hearst has provided funds for the erection of a building for the department of botany in the University of California.

THE ROYAL SOCIETY has awarded a medal to Mr. Horace T. Brown for the work on the chemistry of carbohydrates and on the assimilation of carbon dioxid by green plants.

THE LONG PROMISED English translation of Schimper's *Plant Geography*, by W. R. Fisher, revised and edited by Percy Groom and Isaac Bayley Balfour, is promised for December 15 by the Oxford University Press.

DR. ARNOLD DODEL has retired from the professorship of botany in the University of Zürich. The post vacated will not be filled, but Dr. Alfred Ernst, the assistant, will give instruction in general botany and physiology.

AFTER A short illness the well known systematist, Hofrath Professor C. Haussknecht, died in Weimar on July 7. His large herbarium will be maintained by the family under the auspices of the Thuringian Botanical Society.

ON OCTOBER 25, the twenty-fifth anniversary of Professor Hugo DeVries' appointment as professor of botany at Amsterdam, Professor Went, on behalf of his Dutch friends, presented him with 4250 gulden to be devoted to the further study of mutation.

UPON INVITATION the Botanists of the Central States will meet at St. Louis during the annual meeting of the A. A. A. S., December 28, 1903, to January 2, 1904. A business meeting of the society will be held on the morning of December 30, at a place and hour to be announced on the general program.

ACTIVE STEPS are being taken by the Committee of Organization for the international botanical congress at Vienna in 1905 to provide for the discussion, among others, of the nomenclature question, to which the afternoons of the week, June 12–18, are to be devoted. A circular stating the present arrangements has just been distributed, which can be obtained by any who are interested and have not received it by addressing Dr. A. Zahlbruckner, Wien I, Burgring 7, Austria.

HOWELL'S *Flora of Northwest America*, which has been in course of publication since 1897 is now completed. The author has struggled against many difficulties in producing this work, for which he himself has set the type. Those who have used the parts in the field have found it exceedingly useful. The collections of Mr. Howell, containing types of many species, have been acquired by the University of Oregon and he is to be employed in arranging them for use and safe keeping.

THERE IS contained in *Nature* for November 5 an account of the botany at the Southport meeting of the British Association. One morning was devoted to a discussion of heredity, and another to the origin of monocotyledons by the Misses Sargant and Thomas. Professor Farmer gave a semi-popular lecture on stimulus and mechanism. Short abstracts of a number of papers are given. Several botanical excursions were made, especially to the neighboring sand dunes. In the section for Geography there were several papers of botanical interest dealing with plant geography.

THE Society for Horticultural Science was organized September 9, 1903, in the rooms of the Massachusetts Horticultural Society in Boston on the occasion of the twenty-eighth biennial session of the American Pomological Society. The officers are: president, L. H. Bailey; vice-presidents, G. B. Brackett, T. V. Munson, E. J. Wickson; secretary-treasurer, S. A. Beach; assistant secretary, V. A. Clark; executive committee, the president, *ex officio*, L. C. Corbett (chairman), W. R. Lazenby, J. C. Whitten, F. A. Waugh. The object of the society is the strengthening of horticultural investigation and teaching on its scientific side and the aiding in the development of horticulture as a science. The society is especially designed to meet the professional and technical requirements of horticultural investigators and teachers. The field of the society is clearly defined and heretofore unoccupied. It lies between that of the popular societies on the one hand and that of the societies for general science on the other, and connects them. The programs are to include, besides papers on original investigations, summary presentation of scientific knowledge on special horticultural topics. Some one topic of general and immediate interest is to be made the central feature of each program and is to be announced in advance. The first meeting with a scientific program will be held at St. Louis in Convocation Week, December 28–January 2 next.

GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties, are printed in **bold-face type**; synonyms in *italics*.

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